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G Dallas Hanna (1887–1970)
Diatomist, Geologist, and Invertebrate Paleontologist

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G Dallas Hanna, Diatomist and Invertebrate Paleontologist (1887–1970); Curator of Geology, California Academy of Sciences, 1919-1970

In the early 1920s, G Dallas Hanna established the Academy's diatom collection, reintroducing a tradition for the study of fossil and Recent marine and freshwater microorganisms begun with the founding of the California Academy of Sciences in the early 1850s. Hanna's interest in diatoms began in 1911 during the period when, as an employee of the U.S. Bureau of Fisheries, he was assigned to carry out a fur seal census in the Pribilof Islands. Thus, Hanna, when he came to the Academy in 1919, was to carry on the tradition begun by Academy co-founder John Boardman Trask and Academy member Henry G. Hanks, a tradition he reenergized when he established the first laboratory for micropaleontology on the Pacific Coast.

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Redescriptions of the Nudibranch Genera *Akiodoris* Bergh, 1879 and *Armodoris* Minichev, 1972 (Suborder Doridacea), with a New Species of *Akiodoris* and a New Family Akiodorididae

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The type species of the genus *Akiodoris, A. lutescens*, Bergh, 1880 is redescribed from specimens found in the Sea of Okhotsk, and from the Commander Islands, Russia. A second species in the genus, *Akiodoris salacia* Millen sp.nov., is described from the Pacific waters off British Columbia, Canada. The type species of the genus *Armodoris, A. antarctica* Minichev, 1972 from the Davis Sea, is redescribed from the type and two additional specimens. The relationship of these genera with other genera of phanerobranch dorids is explored and a new family Akiodorididae is formed for the suctorian genera *Akiodoris, Armodoris, Echinocorambe, Doridunculus*, and *Prodoridunculus*.

KEY WORDS: Opisthobranchia, *Akiodoris, Armodoris*, dorid phylogeny, Akiodorididae.

During the second half of 19th and early 20th centuries representatives of phanerobranch dorids of the genera *Akiodoris, Prodoridunculus* and *Doridunculus,* all with a remarkably similar radula, were discovered (G.O.Sars 1878; Bergh 1880; Odhner 1907; Thiele 1912). Bergh (1880) arranged the genus *Akiodoris* within the Suctoria, but *Doridunculus* was placed between the genera *Goniodoris* and *Ancula.* Following this arrangement, Fisher (1883–1887) placed the genus *Doridunculus* within the genus *Goniodoris* and the genus *Akiodoris (*as *Aciodoris)* within the genus *Acanthodoris,* in subgeneric ranks. Bergh (1883) created, for the first time, a phylogenetic scheme for the phanerobranch dorids where both genera *Akiodoris* and *Doridunculus* appeared at the base of Goniodorididae *sensu latu* as descendants of cryptobranch dorids. Later authors usually grouped the genera *Akiodoris, Prodoridunculus* and *Doridunculus* together into the base of the family Onchidorididae, probably considering them the most archaic forms (e.g., Thiele 1931; Odhner in Franc 1968), but Høisæter (1986) arranged *Doridunculus* near the genus *Lophodoris* in the family Goniodorididae. In the second part of last century Minichev (1972) added the genus *Armodoris* as closely allied to *Akiodoris.*

Millen (1987:19), in an abstract referring to a cladistic analysis of the family Onchidorididae, isolated the four genera mentioned above as a separate clade. Martynov (1997) suggested for these genera a new family, Akiodoridae, but he did not give a formal description for this taxon. The main goal of the present study is to revise the two principal genera, *Akiodoris* and *Armodoris,* and to explore their relationship with the families Goniodorididae and Onchidorididae.

The genus *Akiodoris* was erected by Bergh (1879 a) for a phanerobranch nudibranch which has tripinnate gills, a sessile buccal pump, smooth lip cuticle, two cuspidate lateral teeth per side, numerous rectangular marginal teeth, a penis armed with hooks and a vagina containing cilia covered villi. The type species, *Akiodoris lutescens* Bergh, 1880 was found in the Alaskan Aleutians, and this species has not been reported since. One of the authors, Alexander Martynov, found a large number of specimens in several museums and research institutions in Russia, all from the Commander Islands and from the Sea of Okhotsk, mainly in the Kuril Islands. Bergh's (1880) description was based on two specimens, one of which he considered a variety, although why he separated it is unclear. He never illustrated the external features and described them only briefly, although he described the anatomy in detail and included illustrations of some of the organs. A redescription of this species with emphasis on the morphology and additional illustrations of some of the anatomy is included in this paper. Martens (1879) emended the name to *Aciodoris*, replacing the Greek *Akio* (= sharp) with the Latin *Acio*. Because *doris* is a Greek name, we follow the recommendation of the Code that the components of a compound name should agree (Appendix D, II, 11) and revert to the spelling *Akiodoris*. *Aciodoris* is an unjustified emendation under the Code (art.32.5 and 33.2.3) and therefore a junor objective synonym of *Akiodoris*.

The other author, Sandra Millen, found 6 specimens of a small white dorid which possesses the internal characters of *Akiodoris*, in the waters near Vancouver, British Columbia, Canada. These animals differ in a number of external features from *Akiodoris lutescens* and represent a new species belonging to the genus *Akiodoris*. This species is described. and the relationship of the genus to other members of the family is discussed.

The genus *Armodoris* was created by Minichev (1972) for *A. antarctica* Minichev, 1972 from Tokarev Island in the Davis Sea. It has pear-shaped or conical, spiculose tubercles and a radula shape similar to that of *Akiodoris*, but with more teeth. There are up to six inner lateral teeth and up to eight outer lateral teeth per side. The specimen is 16 mm long and sexually mature; it is possibly a mature specimen of *Prodoridunculus gaussianus* as only very small specimens of *Prodoridunculus* have been found. Without having a size range of specimens to examine, we shall retain them as separate taxa. Minichev (1972) separated *Armodoris* from *Akiodoris* because in *Armodoris*, the gonad surrounds the stomach, he observed a single seminal bursa, the spermatheca, on a long duct, and the vagina did not have a villous lining. In our observations of *Akiodoris lutescens*, we found that the stomach is anteriorly buried and posteriorly exposed so that the gonad-covered digestive glands surround it. The spermatheca of *Akiodoris* is short stalked, but has a tubular shape similar to that of *Armodoris antarctica*. *Akiodoris salacia* sp. nov. lacks villi on the vagina. Thus, the taxonomical position of the genus *Armodoris* needs clarification. During a study of the collection of the Zoological Institute RAS (St. Petersburg), two addition specimens of *Armodoris antarctica* were found along with the dissected holotype of *A. antarctica*, which are used here for a redescription of this taxon.

Subclass Opisthobranchia
Order Nudibranchia
Suborder Doridacea
Superfamily Anadoridoidea

Family Akiodorididae Millen and Martynov, fam. nov.
TYPE GENUS: *Akiodoris* Bergh, 1879

Akiodorididae, nom. nudum: Martynov, 1997:233.

DIAGNOSIS. — The notum is spiculose, covered by rounded or elongate tubercles. Posterior part of the notum is round or transformed into two lobes. Branchial pocket is absent, gills are arranged in semicircle with the exception of aberrant *Echinocorambe* where they are reduced to one simple leaf. Head has small four-corned oral veil. Anus dorsal, except for *Echinocorambe* where it is ventral. Buccal pump is a diverticulum of the dorsal surface of the buccal bulb. Peripheral muscle is absent and there are small, separate muscles at the anterior part of buccal pump. Lip disk thin and smooth. Radular formula is 2-14.2-6. 0-1. 2-6. 2-14. Central tooth is usually present, ranging from a small plate to wide arch-shaped structure, sometimes with a central cusp. The first and following up to six lateral teeth have an irregular rectangular base and strong cusp directed downward and several strong denticles on one or both sides. Remaining laterals are in varying degrees of reduction, with a rectangular shape. Receptaculum seminis vaginal or inserted on the uterine duct. Stomach is entirely or partially free from the digestive gland. Prostate tubular or enlarged. Penis with or without spines.

The new family includes the following five genera: *Akiodoris* Bergh, 1879, *Armodoris* Minichev, 1972, *Doridunculus* G.O. Sars, 1878, *Echinocorambe* Valdés and Bouchet, 1998, and *Prodoridunculus* Thiele, 1912.

Genus *Akiodoris* Bergh, 1879

TYPE SPECIES *Akiodoris lutescens* Bergh, 1880, by monotypy

DIAGNOSIS.— The notum is spiculose, covered by rounded tubercles. Posterior part of the notum is round and fully covers the foot and tail. Gills are in a semicircle. Head has a small four-corned oral veil. Anus dorsal. Buccal pump is slightly prominent anteriorly. Radular formula is 8-13.2.1.2.13-8. The central tooth is wide and arch-shaped. The first and second laterals have only 1–2 blunt denticles on both sides. Remaining laterals are in various degrees of reduction. Cerebral and pleural ganglia are fully fused. Stomach is very large and fully free from the digestive gland. Gonad does not cover most of the digestive gland and stomach. Prostate long, tubular. Vagina may have villi. Ejaculatory duct has simple or complex spines.

The genus contains only the type species and the new species described in this paper.

Redescription of *Akiodoris lutescens* Bergh, 1880

(Figs. 1–2)

Akiodoris lutescens Bergh, 1879a:354–355 (*nomen nudum*).
Akiodoris lutescens Bergh, 1879b:4–8 (plates only).
Akiodoris lutescens Bergh, 1880:55–58.

MATERIAL EXAMINED[3].— HOLOTYPE: The type specimen cannot be found in the University of Copenhagen Museum (Kathe Jensen, pers. commun.). OTHER MATERIAL: 1 specimen, 18 September 1949, Shikotan Island, Kuril Islands, Russia, 13.5 m depth, collected by E.F. Gurjanova. 1 specimen, 10 September, 1966, 44°41′N, 148°57′E, 780 m., Segsbee trawl, R/V "Vityaz," St. 5640. Collected by V.M. Koltun. 1 specimen, 31 July, 1971, Vasilieva Pt., Paramushir Is, Kuril Islands, Russia, 20 m depth, large stones, collected by P.G. Kraynyuk. 2 specimens, 5 August, 1970, Gilyak Pt., Paramushir Is, Kuril Islands, Russia, 20 m. depth, rock, collected by A.M. Murakhveri. 1 specimen, 10 August, 1970, Anciferova Is., Kuril Islands, Russia, 15 m depth, large stones, collected by A.M. Murakhveri. 1 specimen, 20 September, 1971, Gromky Pt., Iturup Is., Kuril Islands, Russia, collected by V.I. Lukin. 1 specimen, 20 September 1971, Gromky Pt., Iturup Is., Kuril Islands, Russia, 15 m depth, collected by V.I. Lukin. 1 specimen, 22 September 1971, Shutka Inlet, Iturup Is., Kuril Islands, Russia, 20 m depth, rock, collected by V.I. Lukin. 1 specimen, 14 July,

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[3] Except as indicated, no specimen numbers are given inasmuch as most are in field station collections.

1972, Korabel'naya Inlet, 1 km to sw of Korabel'ny Pt., Medny Is., Commander Islands, Russia, 20 m depth, collected by V.I. Lukin. 2 specimens, 5 August, 1972, Kozyrevskogo Pt., Paramushir Is., Kuril Islands, Russia, 15 m depth, stones, collected by V.N. Romanov. 1 specimen (juvenile), 5 September 1973, Peregrebnogo Pt., Beringa Is., Kuril Islands, Russia, 20–22 m depth, collected by B.I. Sirenko. 2 specimens, 17 September, 1973, Cherny Pt., Medny Is., Commander Islands, Russia, 10 m depth, rock, collected by B.I. Sirenko. 1 specimen, 31 July, 1978 Iona Is., Okhotsk Sea, Russia, 80 m depth, big and small stones, collected by V.A. Pavlyuchkov. 4 specimens, 11 July, 1985, Lopatka Pt., Kamchatka Peninsula, Russia, 17 m depth, rock and stones, collected by V.I. Shalukhanov. 1 specimen, 10 July, 1985, Vladimira Pt., Atlasova Is., Kuril Islands, Russia, 25 m depth, rock. 1 specimen, ZMMU Lc-25738. 14 July, 1985, Sakhalinsky Bay, 54°57.5.N, 141°01.0.E, 95 m depth, R/V "G. Popov," dredge 5, collected by Yu. I. Kantor. 1 specimen, 4 August, 1985, Okhotsk Sea, 55°26′8″N, 145°55′3″W, 160 m depth, stones, collected by A.V. Smirnov. 1 specimen, 20 Aug. 1986, Gladkovsky Pt., Medny Is., Commander Islands, Russia, 10–12 m depth, rock, collected by V.V. Oshurkov. 1 specimen, 25 August, 1986 Monati Pt., Beringa Is., Commander Islands, Russia, 25 m depth, rock, collected by V.V. Oshurkov. 1 specimen, 22 July 1991, Podutesnaya Inlet, Beringa Is., Commander Islands, Russia, 20 m depth, rock, collected by V.I. Shalukhanov. 2 specimens, 14 August 1991, Buyan Pt., Beringa Is., Commander Islands, Russia, 10 m depth, rock, collected by V.I. Shalukhanov. 1 specimen, 23 July 1992, Sivuchy Kamen' Kekur Islet, Medny Is., Commander Islands, Russia, 20 m depth, rock, collected by K.E. Sanamyan. Specimens in Kamchatka's Institute of Ecology and Environment, Petropavlovsk-Kamchatsky, Russia, the Institute of Marine Biology, Vladivostok, Russia, the Zoological Institute, Saint Petersburg, and in the Zoological Museum, Moscow State University, Russia. 1 specimen, 11 July, 1985, Lopatka Pt., Kamchatka Peninsula, Russia, 17 m depth, rock and stones, collected by V.I. Shalukhanov.

EXTERNAL MORPHOLOGY.— The body is elongate-oval and reaches a maximum preserved length of 40 mm (Fig. 1A). The dimensions of one specimen are 40 × 25 × 13 mm. The mantle edge is 4–5 mm, barely covering the sides and tail in preserved animals, although the tail probably extends beyond the mantle in live animals. The notum is densely covered with differentially sized tubercles. The small tubercles, up to 0.4 mm in width, are conical or spindle shaped, the large tubercles, up to 1.4 mm in width, are rounded or cylindrical with round tips (Fig. 1B). Spicules lie in the notum radially around the tubercles, most of the spicules in the tubercles have been dissolved by formalin but traces remain, radiating loosely from the centre outward. The rhinophores have 10–15 lamellae and numerous spicules. The rhinophores contract into openings which do not have raised sheaths but are edged all around with 11–12 large tubercles. There are 10–17 tri- or quadripinnate gills which contract into depressions arranged in a broad horseshoe, which is broken posteriorly by a few tubercles. The gill size decreases towards the posterior, but sometimes a few small tripinnate gills are present anteriorly between the larger gills. Within the gill circlet are many large and some small tubercles, about 80 in total. The anal opening is not raised and is slightly left of centre towards the posterior end of the circlet.

The color in life, according to Dall, is light yellow (Bergh 1880). Preserved specimens are dirty white or pinkish-tan.

The head is veliform, not high, and slightly narrower than the foot. The mouth opening is round and the rounded tentacles are thicker on the anterior edge (Fig. 1C). The foot is broad and bilabiate anteriorly, posteriorly it extends into a small leaf-like tail, which is papillate on the dorsal surface.

ANATOMY.— The oral tube is short and muscular. The anterior half of the buccal bulb has a poorly developed, sessile, rounded buccal pump (sucking crop) with no median muscular band

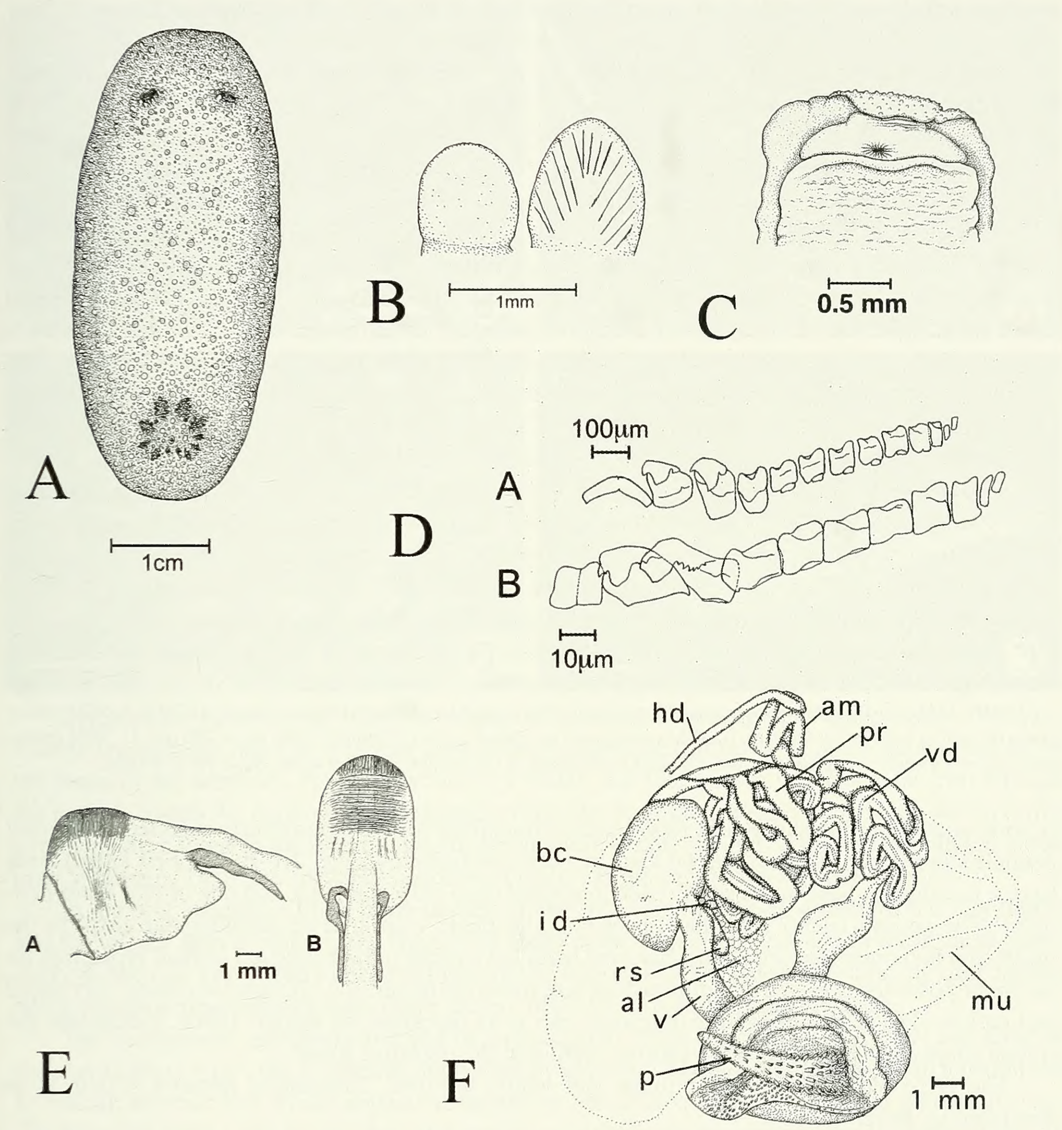

FIGURE 1. *Akiodoris lutescens*, drawn with a camera lucida. A. Whole animal, dorsal view. B. Tubercles, one showing traces of spicules. C. Head and anterior of foot. D. Radula, one half row and rachidian tooth. A. adult, B. juvenile. E. Buccal bulb, A. lateral view B. dorsal view. F. Reproductive system. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; hd, hermaphroditic duct; id, insemination duct; mu, mucous gland; p, penis; pr, prostate; rs, receptaculum seminis; v, vagina; vd, muscular vas deferens.

(Figure 1E). The anterior part of the buccal pump has longitudinal muscular fibres, followed by a band of transverse fibres which extends down the sides of the buccal bulb. Posteriorly there are three longitudinal bands of muscles on each side of the esophagus. Ventrally there is a small posteriorly projecting radular sac. The round lip disk is muscular with a thick outer layer, smooth and yellowish in color. This outer layer is fleshy with only a thin cuticle coating. The radula has 52–69 rows of reddish brown teeth with the formula (8-13.2.1.2.13-8) (Figs. 1D, 2A–B). The central tooth

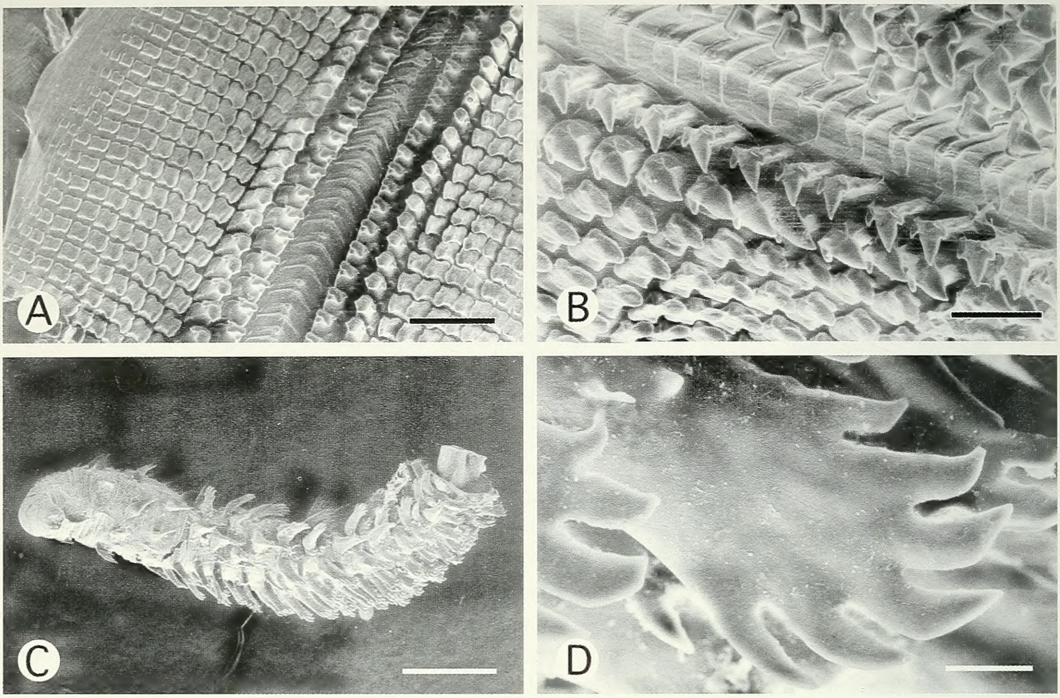

FIGURE 2. *Akiodoris lutescens*. Specimen from Lopatka Pt., tip of Kamchatka Peninsula, Russia, 11/7/85. A. SEM micrograph of radula, scale bar = 400 μm. B. SEM micrograph of central region of radula. Scale bar = 200 μm. C. SEM micrograph of entire penis. Scale bar = 1 mm. D. SEM micrograph of one posterior penial spine. Scale bar = 40 μm.

is wide and flat in the shape of a raised arch. Sometimes a small, posteriorly directed, chitinised denticle can be seen. The two lateral teeth per side can be seen in Fig. 2A–B. The first lateral teeth have a rectangular base and a short, wide, recurved cusp with one inner and one or two outer denticles. The second lateral teeth have a rectangular blade with a large quadrangular cusp on the inside and 5–6 outer denticles. The marginal teeth have rectangular bases and a small projection on the inner posterior corner. They diminish in size towards the outside, the last two being very small and narrow. The remainder of the digestive tract is as described by Bergh (1880), except that the ribbon shaped salivary glands are shorter, ending at the digestive gland.

The large blood glands are pinkish, not white, in color. The central nervous system is as described by Bergh (1880).

The reproductive system is shown in Figure 1F. Bergh (1880) described this system well although he only illustrated portions of it. The vagina is lined by villi, 0.6–0.8 mm long, with a dense axis and non glandular, ciliated epithelium. The penis in Bergh's specimen was retracted, the glans only partly everted. A fully everted penis is shown in Figure 2C and a closeup view of a posterior penial spine in Figure 2D. The reproductive openings are located on the right side about one third of the body's length from the anterior mantle edge. The surface around the genital openings is covered with numerous soft villi approximately 0.3 mm in length.

NATURAL HISTORY.— The known range is expanded from its original localities of Atka Island and Kyska Island in the Aleutians, westward and northward to the Commander Islands, southward along the Kamchatka peninsula and down the chain of Kuril Islands to Shikotan near Hokkaido and into the Sea of Okhotsk to Iona Island near its centre and Sakhalinskiy Bay in the west. It has been collected from low water line to depths of 780 m, usually between 10 and 25 m in the months of July, August and September. The only juvenile was collected in September. All specimens have been collected from rocky areas.

Akiodoris salacia Millen, sp. nov.

(Figs. 3–4)

Akiodoris sp. 1 Behrens, 1991:51, #68

ETYMOLOGY.— Named for the Roman sea-goddess Salacia, wife of Neptune.

MATERIAL.— HOLOTYPE: California Academy of Sciences, CASIZ 110807, 14 September 1985, Tyee Point, Copper Cove, British Columbia, Canada (49°22′8″N, 123°16′5″W), 20 m depth, on hydroids, rocky substrate, collected by S. Millen. PARATYPES: Royal British Columbia Provincial Museum, RBCPM 005-000013-001, 1 specimen, collected with the holotype. Zoological Museum of Moscow University, ZMMU, LC-25737, 1 specimen, collected with the holotype.

EXTERNAL MORPHOLOGY.— Preserved specimens of this small dorid range in length from 4 to 6.5 mm. The largest animal measures 6.5 × 3 × 2.5 mm (l × w × h). The body shape (Fig. 3A) is elongate-oval, wider in front than behind, with a slightly trailing tail. The mantle margin is fairly wide, covering the high sides and head but not the tail. Posteriorly, above the tail, the marginal edge is indented. The notum bears elongate, slightly inflated, spear shaped tubercles with pointed tips (Fig. 4A). There is little variation in tubercle size, which ranges from 0.08 to 0.4 mm in height and 0.06 to 0.18 mm in width. The numerous tubercles are spaced evenly over the notal surface, with a few small ones in the mid-dorsal area and some medium sized ones near the mantle edge.

Spicules are found in the lower ¾ of each tubercle, and their tips protrude slightly. The protruding spicules are rod-like, slimmer than those forming the central shaft inside each tubercle. At the bases of the tubercles, spicules extend in a radial, star-like pattern which can be seen through the notum. Within the notum there are scattered spicules forming a mesh-like network which forms a radial pattern towards the mantle margin. This pattern is only visible on the ventral surface of the mantle margin. There are scattered quadrate spicules stiffening the sides of the body.

In the foot, spicules form a mesh pattern on the sole, and the dorsal surface of the foot flange and the tail are heavily spiculated. Numerous sharp pointed spicules protrude in these areas, especially on the tail. The slightly raised margins of the rhinophores each bear 4–5 tubercles, the largest being the innermost anterior one. There are no tubercles within the branchial arch.

The rhinophores are sturdy and end in a rectangular, blunt tip. The stalk is short and most of the clavus bears wide, thick lamellae supported by spicules. The 8–10 lamellae are attached along a vertical, anterior line which appears inset due to the sudden indentation of the wider lamellae. The lamellae slope ventrally and become narrower towards the posterior where they meet forming a chevron.

The 4–6 contractile gills are bipinnate and incompletely tripinnate, non-retractable, separated on the outside, but joined at their bases towards the inside. They are arranged in a semi-circle which is open posteriorly. The gills are largest anteriorly and directed towards the posterior. The gills are surrounded by tubercles, but none are within the small semicircle. The anus is at the posterior end of the gill arch.

Living specimens (Fig. 3A) are white or faintly yellow in color. There are sometimes a few opaque white specks in the dorsum along the sides and in front of the rhinophores. In immature animals the central area appears pinkish due to the underlying color of the reddish-brown digestive gland. In more mature animals, the digestive gland is covered by creamy-yellow gonads giving the central area a peach hue. Ventrally the digestive gland shows only faintly through the foot. The

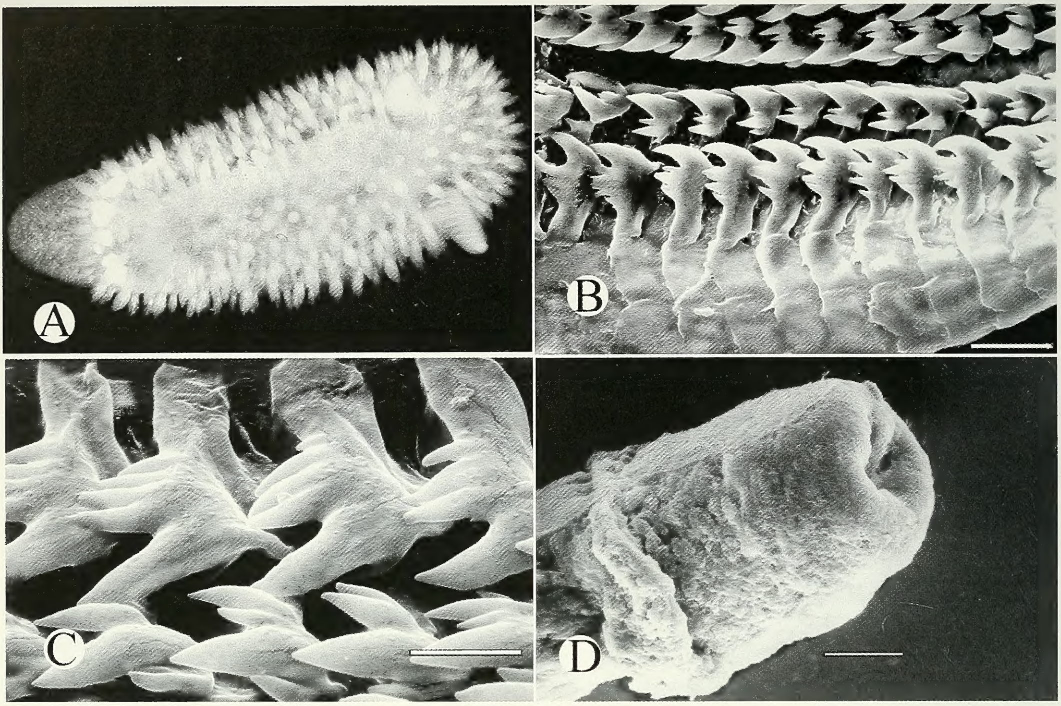

FIGURE 3. *Akiodoris salacia* sp. nov. Specimen from Tyee Pt., near Vancouver, British Columbia, Canada, 14/9/85. A. Photograph of a live specimen of *A. salacia*, 4.6 mm in length. B. SEM micrograph of the radula. Scale bar = 20 µm. C. SEM micrograph of the lateral teeth. Scale bar = 10 µm. D. SEM micrograph of the penis. Scale bar = 40 µm.

anterior edge of the foot and the head are sometimes pale yellow. The rhinophores are pale yellow and the gills are pale yellow or white. An unusual feature of this species is a series of opaque white, round, granular glands along the overhanging posterior border of the mantle. There are 8–10 of these glands, the smallest being located on the midline.

The head (Fig. 4B) is composed of two triangular lobes which end in flap-like tentacles separated from the rest of the head by a dorsal groove. The foot is narrow and elongate, wider and truncate anteriorly. The anterior edge is bilabiate. The triangular tail protrudes up to 0.5 mm. It is thick but does not have a dorsal keel. Noteworthy are its many, posteriorly projecting spicules.

ANATOMY.— The oral tube is a muscular ring with short labial glands surrounding it. The buccal bulb (Fig. 4C) has a dorsal, rounded, sucking crop which is sessile, with no median muscular band and weak peripheral muscles. The radular sac is short and protrudes from a wide, muscular odontophore. The round lip disk is thinly cuticularized and smooth.

The radula has 35–39 tooth rows. The radula formula is 3-5.2.1.2.5-3 (Figs. 3B–C, 4D). There is no well-developed rachidian tooth but the central area has a thickened, raised plate which begins at the fourth or fifth tooth row. The plate is 3–6 µm long. The innermost lateral tooth has a rectangular base and a large, recurved, pointed cusp. It has one inner and two or three outer, well developed denticles. These laterals range in width from 12.5–24 µm and 13–19 µm in length. The outer lateral teeth have a rectangular base with a large, recurved hook on the inside and three or four well developed outer denticles. The outer laterals are 18–19 µm wide and 12–18 µm long. Each marginal tooth is a flat, rectangular plate with slightly rounded outer corners and a small spine on the inner posterior corner. The marginal teeth diminish in width towards the outside. The marginal

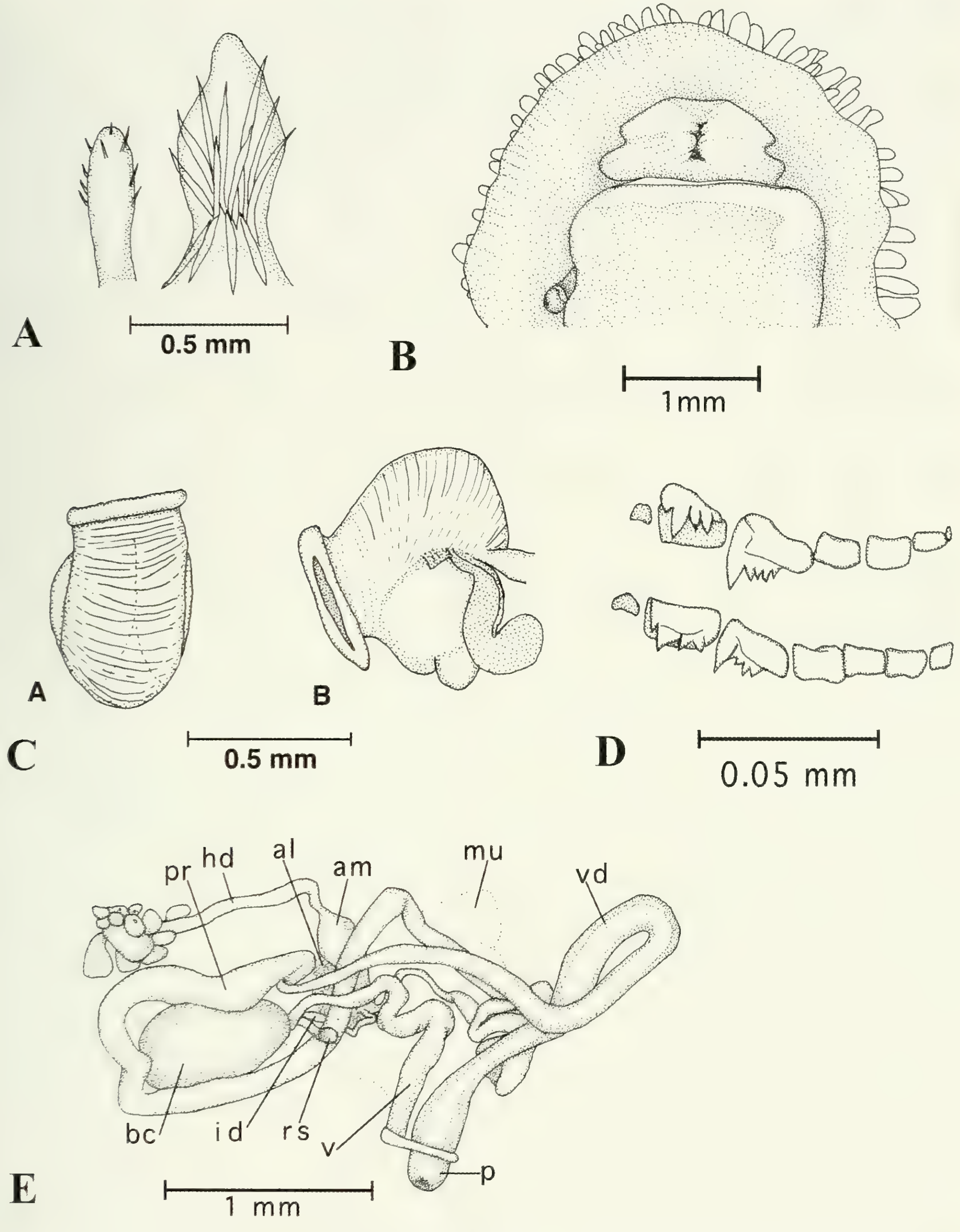

FIGURE 4. *Akiodoris salacia*, drawn with a camera lucida. A. Tubercles, one showing internal spicules. B. Head and anterior of foot. C. Buccal bulb. A. dorsal view, B lateral view. D. Radula. One half row including rachidian plate. E. Reproductive system. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; hd, hermaphroditic duct; id, insemination duct; mu, mucous gland; p, penis; pr, prostate; rs, receptaculum seminis; v, vagina; vd, muscular vas deferens.

teeth range in width from 6–19 µm and in length from 6–10 µm.

The salivary glands are small, flattened, elongate-oval masses lying under the buccal bulb and attaching to it at the anterior end of the esophagus (Fig. 4C). The esophagus is a narrow tube which becomes slightly wider and softer before entering the digestive glands. The digestive glands appear as one elongate mass, wider in front than behind and truncated on the anterior right side. The stomach is sac-shaped, almost entirely separated from the digestive glands. It has a small, round caecum on the right border of the anterior part of the stomach, tucked in the loop of the intestine. The intestine is broad and runs to the right of the midline curving inward to the anus. The anal opening is not raised.

The pericardial sac contains a posterior, thin-walled, triangular auricle and a smaller, more muscular, diamond shaped ventricle. The flattened, compact blood glands are located just posterior to the central nervous system.

The fused cerebro-pleurals are oval and joined by a short commissure. The olfactory nerves have bulbous bases with small attachment points. The large, black eyes have very short stalks. The oval pedal ganglia, smaller than the cerebro-pleurals, are located directly below them and are connected to them by a short commissure. They are connected together by a commissure which is slightly longer than the cerebral one. The small oval, paired buccal ganglia adjoin each other.

The reproductive system is illustrated in Figure 4E. It lies on the right side with the loop of the vas deferens extending from the region of the mouth to a short distance in front of the gills. The ovotestis consists of oval, creamy-yellow lobules lying on the dorsal and lateral surfaces of the digestive glands. The branched gonoducts are broad bands which unite to form one central pre-ampullar duct. This duct widens slightly into a tubular ampulla. There is a short post-ampullar duct which bifurcates into an oviduct and a long vas deferens. A short distance from its origin, the vas deferens becomes prostatic, loops posteriorly towards the ovotestis, encircles the bursa copulatrix and continues anteriorly. It then becomes non-prostatic, loops back on itself and bends downward. The long, tubular, non-prostatic portion enlarges slightly to form a penal bulb containing the uncoiled vas deferens. The penis joins a common atrium with the vagina. It is a cylindrical papilla. Inside, the distal portion of the vas deferens is weakly chitinised and has small spines, 5–8 µm in length. The penis (Fig. 3D) is eversible, but the spines were not everted on any of the specimens.

The vagina is long and cylindrical, wider near its opening posterior to the penis in the common atrium, and gradually narrowing. It loops back on itself and then gives off a short duct to the large, round bursa copulatrix. The insemination duct, after a short distance, is joined by a short duct from the tubular receptaculum seminis. The insemination duct is long and winding. It terminates at the oviduct near its junction with the post ampullary duct and entrance to the female gland mass.

The female gland mass has an oval, yellow albumen gland. The hermaphroditic ampulla runs down its anterior surface.Surrounding it, anteriorly, posteriorly, and on the inner side is a white mucous gland. The separate oviductal opening is ventral to the common genital atrium. The two reproductive openings are located high on the right side about ⅓ of the body's length from the anterior mantle edge.

Natural History.— The specimens described in this paper were found in September at a depth of 20 m. on a rocky bottom swept by moderate currents. They were all found on an old hydroid colony intermingled with the ctenostome bryozoan *Farrella elongata*, which is presumed to be their food. The larger specimens had partially mature reproductive systems and were copulating, but no spawn was present or laid in the laboratory during the week subsequent to their capture.

Remarks.— The newly described species is placed in the genus *Akiodoris* Bergh, 1879 because it has a nearly identical reproductive system, bi- and tripinnate gills, smooth lip disk, sessile pharyngeal bulb, stomach which is free from the digestive glands, digestive caecum, and armed penis. However, in the presence of a slight posterior mantle reduction and gills arranged in a small, non-tuberculose semi-circle with a posterior anus, *A. salacia* is more similar to the genus *Doridunculus*. We considered this similarity as superficial due to the small size of *A. salacia* and relative frequency of appearance of a pair of lobe-like structures in the posterior part of the notum in phanerobranch dorids, apparently caused by partially delayed ontogenetic processes in notum formation.

There are a number of differences between *Akiodoris lutescens* and *A. salacia*. Externally, the tubercles differ in that *A. salacia* has long, similar sized, lanceolate tubercles with projecting spicules, whereas *A.lutescens* has smaller, conical and rounded tubercles of varying sizes. In *A. salacia*, the gill opening is in a small semi-circle with no enclosed tubercles and the anus is at the posterior edge. In *A.lutescens*, the gill pocket forms a large horseshoe enclosing many tubercles and the anus. The posterior mantle margin is slightly indented in the new species, but this does not appear to be the case in *A. lutescens*. Both species have a flat leaf like tail which is dorsally spiculated. The distinctive mantle glands of *A. salacia* can only be seen in live specimens, so their presence cannot be used as a distinguishing feature. Only preserved *Akidoris lutescens* have been observed. Internally, the radula has fewer (4–5) marginal teeth than a similar sized (6 mm) juvenile *A. lutescens*, which had 7–9 marginal teeth (Fig.1D). The thickened cuticular central tooth observed in specimens of *A. salacia*, is not well developed, but it may develop in older specimens. Only in larger *A. lutescens* does the central cuticle form a chitinised spine on the rachidian tooth. The central nervous system of the two species varies in that the eyes are large and sessile in *A. salacia* and smaller and on long stalks in *A. lutescens* and the unusual lateral position of the pedal ganglia found in *A. lutescens* was not found in *A. salacia*.

Genus *Armodoris* Minichev, 1972

TYPE SPECIES *Armodoris antarctica* Minichev, 1972, by monotypy

DIAGNOSIS.— The notum is spiculose, with rounded tubercles. Posterior part of the notum is round and fully covers the tail. Gills are in a semicircle. Head has a small four-corned oral veil. Anus dorsal. Buccal pump is oval and prominent. Radular formula is (4-8.4-6.1.4-6.4-8). The central tooth is a square plate of moderate size with a slightly prominent central cusp. The lateral teeth have a rectangular base and one long cusp to the inside of center. Denticles are found on the first 6 teeth, the outer 4–8 have one reduced cusp or are reduced to rectangular bases. Cerebral and pleural ganglia are fully separated. Only a small dorsal part of the stomach is free from the digestive gland. Gonad covers most of the digestive gland and stomach. Prostate massive. Interior of vagina is simple. Ejaculatory duct has simple spines.

The genus contains only the type species.

Redescription of *Armodoris antarctica* Minichev, 1972

(Figs. 5–6)

Armodoris antarctica Minichev, 1972:366–368, fig 4; Cattaneo-Vietti et. al., 2000:175.

TYPE MATERIAL.— HOLOTYPE: ZIN N 1[4] (dissected, most internal organs are removed and are

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[4] ZIN — The Zoological Institute, Russian Academy of Sciences, St. Petersburg; the numbers refer to systematic catalogue, without inventory numbers in this case.

[5] There are no exact data in the first description of *Armodoris antarctica*, nor on the label that accompanies the holotype, except for Minichev's personal label "19-2". The present date, depth and substrata is reconstructed by comparison with neighboring labels "19-1" and "19-3", which both have complete or semi-complete data.

not traceable, radula slide not found), around January 19, 1966[5], 11th Soviet Antarctic Expedition, Davis Sea, Tokarev Id., Between Samples 45 and 55, Depth about 30–32 m, rock, collected by A. F. Pushkin. OTHER MATERIAL: 2 specimens (ZIN N 2[4], N 3[4]), Zoological Institute, Russian Academy of Sciences, February 1, 1969, 13th Soviet Antarctic Expedition South Shetland Ids., King-George Id., La Guardia Nacional Bay, transect I, St. XXI, sample 60, 36 m depth, stones, collected by A. F. Pushkin.

EXTERNAL MORPHOLOGY.— Preserved specimens range in length from 13 to 16 mm. The holotype measures 16 × 9 × 5 mm (l × w × h) (Fig. 5 A–C). The specimen, ZIN N 3, is 13 × 7.4 (l × w). The body shape is elongate-oval, slightly wider in front than behind. The mantle margin is amply wide, fully covering the sides and tail. Posteriorly, the marginal edge is without any traces of an indent. The notum bears tubercles of different sizes, scattered small tubercles between the larger ones. In the middle of notum, longitudinally, there are some rather large, pear-shaped tubercles. They become more elongate or cylindrical toward to the notal margins. Tubercles sizes range from 0.07 to 1 mm in height and 0.06–0.7 mm in diameter. Spicules within a tubercle are rod-like, varying in size, nearly straight or slightly crooked. The spicules sometimes slightly extruded through upper part of the tubercle. The margins of the rhinophore pockets are very low and bear 6 blunt tubercles (right side of the specimen ZIN N 3) and 4 in the holotype. The rhinophores have about 10 lamellae.

Six (ZIN N 3) to nine (holotype) contractile, but non-retractile, gills are unipinnate and incompletely bipinnate (Fig. 5D). They are arranged in a semi-circle, which is posteriorly completed by a large tubercle. The gills are surrounded by elongate tubercles. The holotype and ZIN N 2 specimen have three tubercles inside the gill semicircle, whereas example ZIN N 3 has none. The anus is in front of the posterior tubercle in the 13-mm length specimen. Preserved specimens are whitish-pinkish or yellowish.

The head is a small semi-oval oral veil with two short blunt lobes extending posterio-laterally (Fig. 6C) The foot is rather wide, anteriorly truncated without any traces of post oral lobes. Posteriorly, the foot narrows slightly to form a flat, blunt tail (Fig. 6C).

ANATOMY.— The oral tube is short and muscular. Almost the entire upper part of the buccal bulb has a well-developed, oval buccal pump (Fig. 6E). The buccal pump has no peripheral muscle (median muscular band). The anterior part of the buccal pump has longitudinal muscular fibers, followed by a band of transverse fibers, which extends down the sides of the buccal bulb. The round lip disk is smooth, covered by a colourless cuticle. Radular formula is 36–52 (4-8.4-6.1.4-6.4-8) (Fig. 6D). The central tooth is a thin square plate of moderate size with a slightly prominent central cusp. The inner laterals are denticulate, and they gradually transform to the simple small plates of the outermost laterals. The first and at least 4–5 following laterals have a rectangular base and short or moderately long cusp (cusp of 2nd and 3rd laterals, in general, stronger than first ones) directed downward, usually straight or slightly curved. The first three or four inner laterals have 1–3 denticles on both sides of the cusp, the following 3–5 laterals have a serration (or it is reduced) on the outer side of the cusp. The remaining two to four laterals have a greatly reduced cusp, devoid of denticles, and the outermost tooth is just a simple plate. The elongate-oval salivary glands are small and attach to the buccal bulb at the anterior end of the esophagus (Fig. 6E). The latter is a rather wide, flattened tube. The stomach is sac-shaped, only a small dorsal portion is separate from the digestive gland (Fig. 6B). There is no caecum on the stomach.

The pericardial sac contains a posterior, thin walled narrow-triangular auricle and smaller, oval shaped ventricle (Fig. 6B). The blood glands are slightly visible and located posterior to the central nervous system.

The cerebral and pleural ganglia (Fig. 6B, 6F) are separated and the later are smaller. The

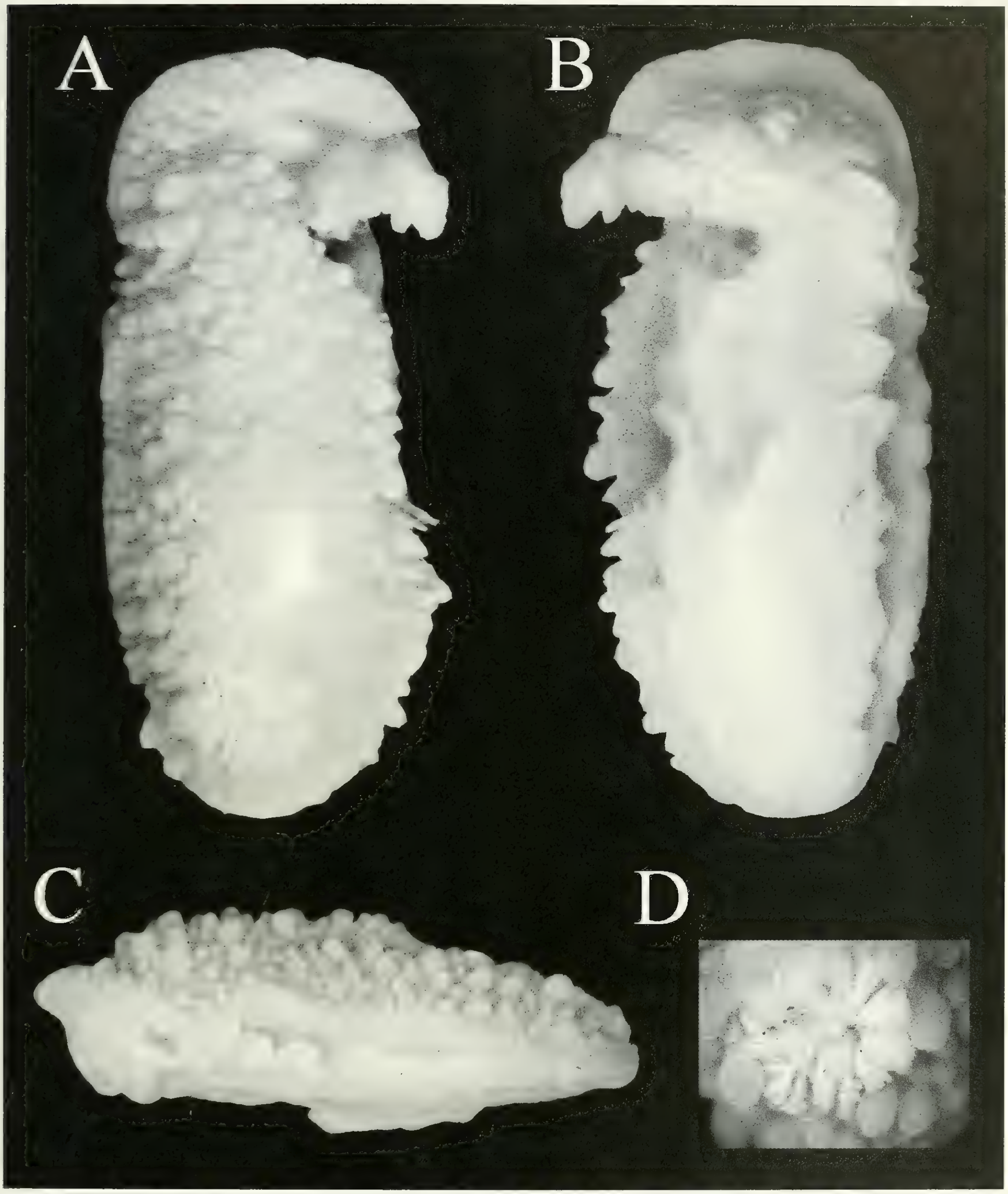
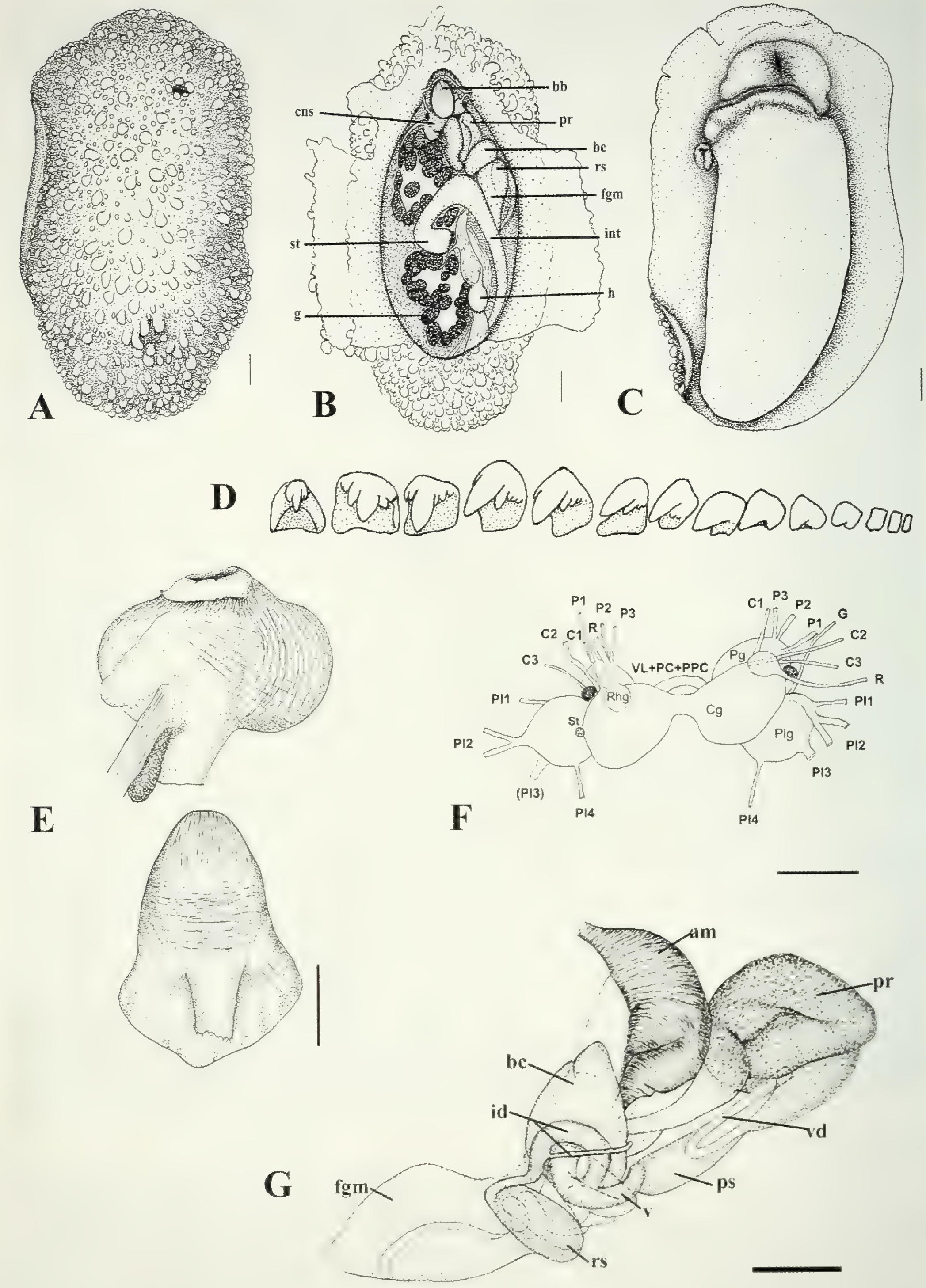


FIGURE 5. *Armodoris antarctica*, holotype. A. dorsal view. B. Ventral view. C. lateral view. D. Close up of the gills and tubercles.

large, black eyes have very short stalks. The pedal ganglia, similar in size to the cerebral, lie below them and are connected to them by short commissures. The rhinophoral ganglia are roundish. The buccal ganglia are roundish-oval. Gastro-esophageal ganglia were not found. In the cerebrals, three pairs of cerebral nerves were detected, in the pleurals, four, and in the pedals, three.

The ovotestis is characterised by large female follicles (Fig. 6B). The ampulla is voluminous


A
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C2
C1
R
C3
VL+PC+PPC
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and kidney-shaped (Fig. 6G). There is a short post-ampullar duct, which bifurcates into an oviduct and a long vas deferens. The pre-prostatic duct is relatively long and wide. The prostatic part of vas deferens is a very massive tangle of a few thick, flattened loops. The prostate doesn't encircle the bursa copulatrix. The vas deferens narrows rapidly to a non-prostatic portion, loops back on itself, and bends downward. The deferent duct is a thin, muscular, not very long, gradually enlarging duct, which widens to an elongate penial bulb. The penial bulb joins a common atrium with the vagina. The ejaculatory duct of vas deferens has inside tiny, densely placed, spines. A partially everted penis is very narrow. The vagina is rather short and wide, similar in diameter its whole length, bending in the middle and entering the large, irregularly-triangular, bursa copulatrix. Villi inside the vagina are absent. The receptaculum seminis is oval and has a long, muscular, gradually widening duct, which joins the middle of the insemination duct. In the holotype, the receptaculum seminis is more elongate. The insemination duct is long, leaving the vagina near the middle and entering the female gland mass near the oviduct.

REMARKS.— The genus *Armodoris* has at least four to six well developed inside lateral teeth and no clear border between inner and outer laterals, whereas the genera *Akiodoris*, *Prodoridunculus* and *Doridunculus* have two well-differentiated inner laterals and rest of the laterals demonstrate reduction. *Echinocorambe* has three inner laterals, markedly different from the outer teeth. The radulas of *A. lutescens* and *A. salacia* are similar in the shape of the two first laterals and in the reduction of most of the outer laterals. This is a parallel case with the genus *Adalaria,* where the first lateral is more or less stable, but outer laterals have tended to reduce. The stomachs of *Akiodoris* and *Doridunculus* are massive and mostly free from the digestive gland, whereas *Armodoris* has a rather small free part of the stomach. *Armodoris* has large female follicles, which may be due to direct embryonic development, but the stomach is not fully surrounded by the gonad, as erroneously reported by Minichev (1972). The ampulla of *Armodoris* is large, more like that of *Doridunculus echinulatus.* Both *Akiodoris* species have similar long, but tubular prostates, whereas the prostate of *Armodoris* is massive. The receptaculum seminis is very narrow and tube-shaped in both *Akiodoris* and *Doridunculus*, but in the King-George's examples of *Armodoris* it is oval and in the holotype it is narrow-oval. The villi of the vaginal duct are not present in *Armodoris.* The buccal pump in *Armodoris antarctica* is more developed, although it has the same structure as found in *Akiodoris*, *Doridunculus* and *Echinocorambe.* Due to above differences between *Armodoris* and the other four genera with similar radular teeth, it is suggested that we maintain the genus *Armodoris.*

Compared to the King George Island examples, the dissected holotype has well preserved gills and oral veil. Minichev (1972) incorrectly interpreted the reproductive system and partially the digestive system of *A. antarctica.* He found only one receptaculum ("spermatheca" in his terms) and although he noted that "a 'spermatocyst' (= bursa copulatrix) is not evident in the present material", nevertheless, he considered this case to be a "unique feature" (Minichev 1972:366). The holotype originated from the Davis Sea, and the two additional specimens originated from another corner of Antarctic, the South Shetland Islands. An additional specimen of *A. antarctica* is the "Italian

FIGURE 6. *Armodoris antarctica* drawn with a camera lucida. A. Dorsal view, scale bar = 1 mm. B. Dissected view, scale bar = 1 mm. Key: bb. buccal bulb; bc, bursa copulatrix; cns, central nervous system; fgm, female gland mass; g, gonad; h, heart: int. intestine: pr. prostate; rs, receptaculum seminis; st, stomach. C. Ventral view, scale bar = 1 mm. D. Radula. One half row including rachidian tooth. E. Buccal bulb, Dorsal and lateral views. Scale bar = 0.5 mm. F. Central nervous system. Scale bar = 0.5 mm. Key: C 1-3, cerebral nerves; Cg, cerebral ganglia; P 1-3, pedal nerves; PC, pedal connective; PPC, pleuro-pedal connective; Pg, pedal ganglia; Pl 1-4, pleural nerves; Plg, pleural ganglia; R, rhinophoral nerve; Rhg, rhinophore ganglia; St, Statocyst; VL, visceral loop. G. Reproductive system. Scale bar= 1 mm. Key: am, ampulla; bc, bursa copulatrix: fgm. female gland mass; id, insemination duct; ps, penis sheath; pr, prostate; rs, receptaculum seminis; v, vagina; vd. muscular vas deferens.

sample" from the stomach of a fish, *Trematomus bernacchii*, caught in the Ross Sea, Terra Nova Bay (Cattaneo-Vietti 2000). By the courtesy of Stefano Schiaparelli, we have studied a SEM image of the radula of the Italian specimen of *A. antarctica*. The radulas of all four specimens of *A. antarctica* are similar. The rarity of *Armodoris antarctica* is caused by its inhabiting only shallow waters on rocky substrates, and it can only be found by diving collections, which is certainly rare in the Antarctic, especially around 30 m (both holotype and two additional samples were collected slightly below 30 m on rocky substrates and in remote localities).

PHYLOGENETIC ANALYSIS

Dorid nudibranchs are currently divided into two groups, those with gills and rhinophores which retract into a closable pocket, the Eudoridoidea (=Cryptobranchia), and those whose gills and rhinophores have no pocket or an open pocket, the Anadoridoidea (= Phanerobranchia). The phanerobrachs dorids were in turn subdivided by Bergh (1892) into two groups, those with a suctorial buccal apparatus (suctorians) and those without (non-suctorians). These are informal groups, but the three families that Bergh placed into the suctorians, Corambidae, Goniodorididae, and Onchidorididae, are commonly arranged together. There have been numerous rearrangements within these three families over the years, but currently the family Onchidorididae is believed to contain the genera *Acanthodoris, Adalaria, Akiodoris, Arctadalaria, Armodoris, Calycidoris, Diaphorodoris, Doridunculus, Onchidoris* and *Prodoridunculus*, although Wägele and Willan (2000) consider the genera *Akiodoris* and *Armodoris* to belong to the Goniodorididae following Bergh (1883), who placed them at the base of the Goniodorididae.

Four of these genera form a distinct clade based primarily on their radular characteristics (Millen 1987). Most genera in the family Onchidoridae have on each side a single, large, strongly hooked lateral with a triangular base and narrow, hooked, marginal teeth. The rachidian, where present, has an elongate, rectangular shape. In contrast, a clade of four genera, *Akiodoris, Armodoris, Doridunculus,* and *Prodoridunculus*, have two or three (sometimes up to 6), wide, rectangular lateral teeth per side. The first lateral has internal and external denticles, the second and third, when present, have external denticles. The rachidian tooth, if present, is arch-shaped. The marginal teeth are wide and rectangular with a small hook. These four genera also have a relatively simple buccal pump.

Recent cladograms using either molecular or morphological data, which have included a variety of cryptobranch and phanerobranch dorids, have suggested that the phanerobranch dorids may, in fact, be polyphyletic (Wollscheid and Wägele 1999; Wägele and Willan 2000; Wollscheid-Lengeling et al. 2001; Vallès et al. 2001; Váldes 2002). These studies have not shown suctorian dorids to be polyphyletic, nor have they been able to use the full range of genera in the family Onchidoridae. The genera used were those with hook-shaped teeth, *Acanthodoris, Adalaria, Calycidoris, Diaphorodoris,* and *Onchidoris*, which generally clustered together. To observe the characters which distinguish *Akiodoris* and *Armodoris* from other genera and to establish their closest relationships, and to which family they should be assigned, we produced a cladogram using all of the possible Onchidorididae genera. These were compared to sister taxa consisting of three genera from the Corambidae (*Corambe*, Loy and Echinocorambe) and one Goniodorididae (*Goniodoris*). One cryptobranch dorid, family Chromodorididae (*Cadlina*), was used as a sister taxa to the phanerobranchs. The outgroup and basal rooting was based on the basal Anthobranchiate dorid genus *Bathydoris*, using *B. spiralis* Valdés, 2002, which is closest to the cryptobranch and phanerobranch dorids (*fide* Valdés 2002). In total, 15 taxa and 29 characters were analysed using MacClade and PAUP 3.1.1.

The 29 characters used in this analysis are listed below: 23 characters are binary and 6 are multistate. Character states are indicated by numbers; 0 is the plesiomorphic condition and 1–2 are apomorphic. Non-applicable and unknown characters are coded with a ?. Polarities are the result of outgroup comparison. Table 1 (see Appendix) shows the distribution of plesiomorphic and apomorphic states.

1. *Mantle rim*: The mantle rim (projecting edge) is narrow, partially absent in *Bathydoris* and some phanerobranch dorids (0) whereas it covers the sides and foot in most dorids (1).
2. *Posterior mantle rim*: The posterior mantle rim, where distinct, is usually entire in *Bathydoris* and most dorids (0). It is bilobed in some phanerobranch dorids (1).
3. *Tail*: The tail is extended in *Bathydoris* and some phanerobranch dorids (0). It is small and covered by the mantle in most dorids (1).
4. *Ridge on tail*: The tail is usually smooth in *Bathydoris*, cryptobranch dorids and most phanerobranch dorids (0). It has a mid-dorsal crest or ridge in some phanerobranch dorids (1).
5. *Notal spicules*: Some *Bathydoris* and most dorid nudibranchs have integumentary spicules in the notum (0). These are absent in a few dorid species (1).
6. *Notal sculpture*: Sculpture in the form of deciduous villi is present in *Bathydoris* (0); most species of dorid nudibranchs have well attached tubercles (1). Only a few species are smooth (2).
7. *Head*: The head in *Bathydoris* and most phanerobrach dorids is veliform (0). Cryptobranch dorids have a round head and separate tentacles (1).
8. *Rhinophore sheath*: *Bathydoris* and some phanerobranch dorids have rhinophores which lack sheaths and are attached directly to the dorsum (0). Other phanerobranch dorids have non-contractile sheaths into which the rhinophores can retract (1). Cryptobranch dorids have contractile rhinophore sheaths which close over retracted rhinophores (2).
9. *Rhinophores*: *Bathydoris* and most other dorids have lamellate rhinophores (0). A few dorids have smooth rhinophores (1) which may have vertical envelopes (2).
10. *Gill protection*: *Bathydoris* and some phanerobranch dorids have gills which lack sheaths and are inserted directly on the notum (0). Some phanerobranch dorids have sheaths into which the gills can retract but which do not close over the gills (1). Cryptobranch dorids have contractile gill sheaths which close over the retracted gills (2). For taxa with no mantle gills, this character has been treated as non-applicable.
11. *Gill number*: *Bathydoris* and most dorids have more than five gills (0). A few species of phanerobranch dorids have less than five gills which is considered a reduction (1).
12. *Gill location*: *Bathydoris* and most dorids have the gills located on the mantle some distance from the edge (0). Some phanerobranch dorids have the gills posterior at the mantle edge or below it (1).
13. *Notal sculpture within the gill circlet*: *Bathydoris* and cryptobranch dorids do not have papillae or tubercles within the area encircled by the gills (0). Some phanerobranch dorids have notal sculpture in this area (1). For taxa with no mantle gills, this character has been treated as non-applicable.
14. *Anus location*: *Bathydoris* and most dorids have the anus located on the mantle some distance from the edge (0). Some phanerobranch dorids have the anus posterior at the mantle edge or below it (1).
15. *Lip disk*: *Bathydoris* has thick chitinous labial armature and other dorids may have various rods or papillae to strengthen the lip disk (0); a smooth, thin cuticle is considered apomorphic (1).
16. *Buccal pump*: A sucking pump on the pharynx is absent in *Bathydoris*, non-suctorian

phanerobranch dorids and cryptobranch dorids (0). This pump distinguishes the suctorian phanerobranch dorids (1).

17. *Peripheral muscles*: A median longitudinal band of muscles is not found on the phanynx of *Bathydoris* and most dorids (0). This muscle is found on some of the suctorian phanerobranch dorids (1).

18. *Rachidian tooth*: A rachidian tooth is present in *Bathydoris* and some dorids (0). Many dorids have lost this central tooth (1).

19. *Number of teeth per half row*: Primitive dorids and *Bathydoris* have many teeth, >10, per half row (0). Reduction has resulted in narrower radulas with fewer than 10 lateral teeth (1).

20. *Number of inner laterals*: Inner lateral teeth tend to be more highly developed than the outer lateral (marginal) teeth which are often reduced. In *Bathydoris*, and some dorids, only the first lateral tooth differs from the outer lateral teeth (0). In other dorids there are 2 or more teeth which can be differentiated from the outer laterals (1).

21. *Shape of innermost lateral tooth*: *Bathydoris*, some cryptobranch and some phanerobranch dorids have cuspidate innermost lateral teeth. The cusp is towards the center of a broad tooth and denticles may appear on one or both sides (0). Other, phanerobranch dorids have beak-like teeth, with a long cusp on the outer edge, and denticles, when present, only on the inner side (1).

22. *Denticulation on innermost lateral tooth*: *Bathydoris* has denticulations on both sides of the inner lateral teeth, as do some dorids (0). Other dorids, used here, may have denticulations only on the inner side (1) or they may be absent (2).

23. *Marginal teeth or outer lateral teeth*: In *Bathydoris* and many cryptobranch dorids, these are elongate, hamate teeth, with or without denticles on the outer side (0). In some phanerobranch dorids they are reduced to either an elongate-oval plate (1) or a wide, rectangular plate (2).

24. *Ampulla*: The hermaphroditic ampulla is narrow and undifferentiated in *Bathydoris* and many dorids (0). It is wide and usually short in some dorids (1).

25. P*enial spines*: Spines on the eversible vas deferens of the penis are absent in *Bathydoris* and some dorids (0). Small spines are present in a number of dorids and their presence is considered an apomorphy (1).

26. *Seminal receptacle*: This sac for sperm storage is absent in most *Bathydoris* species, but present in *Bathydoris spiralis* as a small sac with one duct (stalked) (0). In some dorids, it has two ducts (unstalked), which is considered derived (1).

27. *Seminal receptacle insertion*: This sac is inserted by its duct on the vagina in *Bathydoris spiralis* and many other dorids (0). In some dorids, it is inserted part way along the insemination (uterine) duct (1).

28. *Oviduct*: The oviduct carrying the eggs usually passes directly into the female gland mass (0). In a few dorids, it enters the seminal receptacle before entering the female gland mass, which is considered apomorphic (1).

29. *Cerebro-pleural ganglia*: These ganglia are separate in *Bathydoris* and a few dorids (0). They are fused in most dorids (1).

Phylogenetic Results

The data matrix results in one tree (Fig. 7), 64 steps long, with a consistency index of 0.562 and a retention index of 0.692. The Bremmer support index values (values to the right of the line in Fig. 7) show that most of the branches are poorly supported, with the exception of the clade containing those phanerobranch dorids with beak-shaped laterals (value 2) and the node containing Corambe and Loy (value 2+).

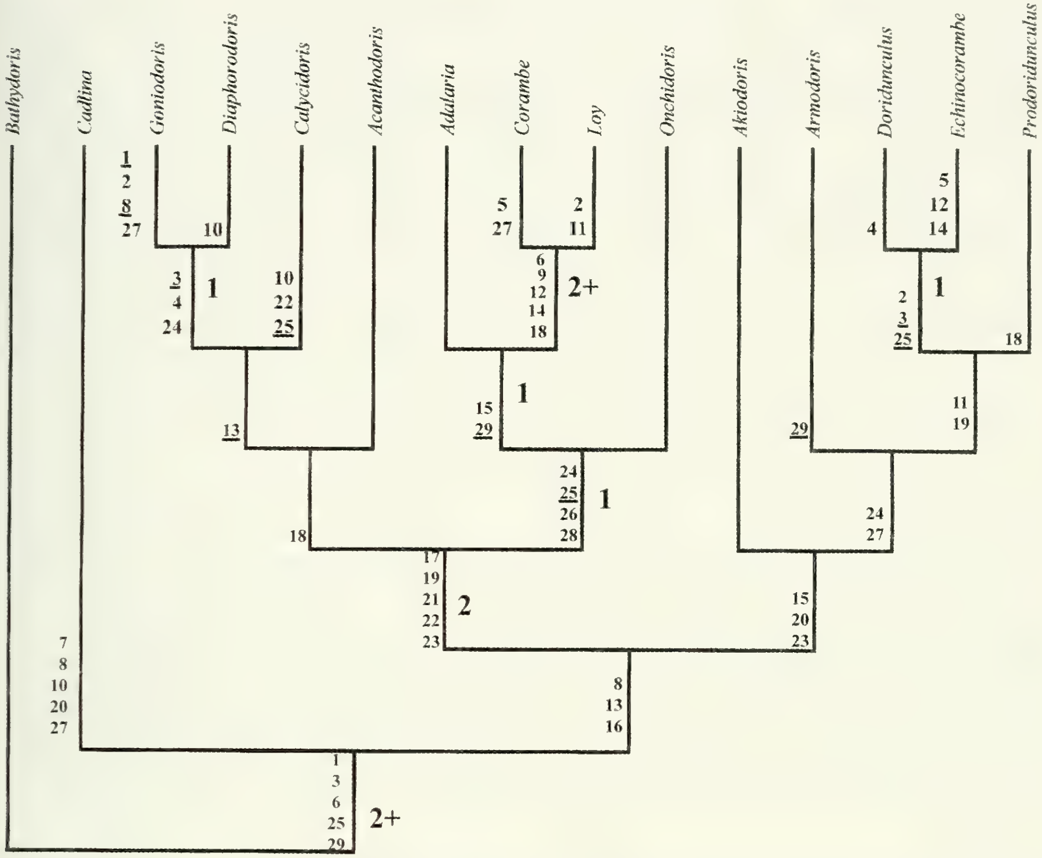

Figure 7. Strict consensus tree of a preliminary phylogeny. Apomorphies are indicated by character numbers included in the analysis. Characters which exhibit reversal are underlined. Bremer support values are 0 unless indicated by large numerals on the right side of the nodes.

In the resulting tree, the cryptobranch dorid *Cadlina* separates as a sister group to the remaning suctorian phanerobranch dorids, which are supported by the synapomorphies of non-contractile rhinophore sheaths (#8), the presence of papillae within the gill circlet (#13) and the presence of a buccal pump (#16).

These suctorian phanerobranch dorids traditionally belong to three families, Corambidae, Goniodorididae and Onchidorididae, but some members of the three families clustered together into one clade. This clade is distinguished by the presence of a peripherial muscle in the buccal pump (#17), a reduced half row of the radula (#19), one inner lateral tooth (#22), beak-shaped inner laterals (#21), and elongate oval outer laterals (#23). The Corambidae nests within the Onchidorididae and the genus *Goniodoris* nests with other members of the Onchidorididae and next to *Diaphorodoris*. Already the Superfamily Onchidoridoidea Gray, 1827 has been used to combine family Corambidae and Onchidorididae by Valdés and Bouchet (1998). Our data suggest that the families Corambidae and Onchidorididae are closely related (see Martynov 1994) and should be combined into one family, as suggested by Martynov (1999); the family group name Onchidorididae Gray, 1827 has priority. Further study is needed to clarify the position of *Goniodoris* and other members of the Goniodorididae in relation to this family.

The second clade contains members of the 'basal' Onchidorididae, which have sometimes been placed into the Goniodorididae. In this clade are the genera studied in this paper, *Akiodoris* and *Armodoris*, together with the closely related *Doridunculus* and the poorly known *Prodoridunculus*. Another poorly known genus, *Echinocorambe*, initially was placed in the family Corambidae by Valdés and Bouchet (1998) inasmuch as it has similar paedomorphic features. It was also suggested by Martynov (2000) that it is close to *Doridunculus* because of its similar radula and buccal pump; it may, in fact, be a juvenile of the latter. The cladogram confirms that it belongs in the same clade as *Doridunculus*. These five genera are in a clade with similar radulas, buccal pumps, and reproductive systems. Synapomorphies which distinguish this clade are the presence of a smooth, thin, lip disk (#15), two or more inner lateral teeth (#20), and the possession of rectangular, reduced outer laterals (#23). The distant position of *Goniodoris* in relation to this clade suggests that these five genera should not be in the family Goniodorididae. This clade forms a sister group to the clade containing the Onchidorididae (including Corambidae) and *Goniodoris*. Thus, this clade is considered a distinct family, Akidorididae Millen and Martynov, fam. nov.

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Appendix

TABLE 1. Data matrix showing the distribution of character states (see text for details).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Bathydoris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cadlina	1	0	1	0	0	1	1	2	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1
Goniodoris	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	0	1	0	1
Acanthodoris	1	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	1	1	0	1	1	1	0	1	0	0	0	1
Adalaria	1	0	1	0	0	1	0	1	0	0	0	0	1	0	1	1	1	0	1	0	1	1	1	1	0	1	0	1	0
Akiodoris	1	0	1	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	1	0	0	2	0	1	0	0	0	1
Armodoris	1	0	1	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	1	0	0	2	1	1	0	1	0	0
Calycidoris	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	1	1	1	1	0	1	2	1	0	0	0	0	0	1
Corambe	1	0/1	1	0	1	2	0	1	1/2	?	0	1	?	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	0
Diaphorodoris	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	0	0	0	1
Doridunculus	1	1	0	1	0	1	0	1	0	0	1	0	0/1	0	1	1	0	0/1	1	1	0	0	2	1	0	0	1	0	1
Onchidoris	1	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	1	1	1	1	0	1	0	1	1
Prodoridunculus	1	0	1	?	0	1	?	1	?	?	1	?	?	?	?	?	?	1	1	1	0	0	2	?	?	?	?	?	?
Echinocorambe	1	1	0	0	1	1	0	1	0	?	1	1	?	1	?	1	0	0	1	1	0	0	2	?	0	?	?	?	?
Loy	1	1	1	0	0	2	0	1	1	?	1	1	?	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	0

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First Hawaiian Record of the Grenadier *Lepidorhynchus denticulatus* (Macrouridae: Gadiformes: Teleostei)

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On August 16, 2003, while night lighting for squid off the northwest coast of Oahu, Mr. Richard Cadaoas caught on hook and line an 18 to 20-inch (about 46–51 cm) squid. In its stomach was a small fish about 20 cm long in excellent condition, having suffered little deterioration from its stay in the squid's stomach. The specimen was taken to Mr. Arnold Suzumoto, Collections Manager for the ichthyological collections of the Bernice P. Bishop Museum, Honolulu. The fish could be readily identified as a grenadier, owing to its long tapered body that ends in a point and lacks a caudal fin, the relative form and positions of the fins, the spinulated body scales, and the general form of the head. The snout in the specimen was narrow and rounded, however, unlike the pointed and often stoutly reinforced snout of most other members of the family (excluding the bathygadids), and none of the ridges on the head were strengthened by stout spiny scutelike scales. The fish did not fit the description of any previously known species from the Hawaiian Islands and was subsequently sent to me, as one of the primary workers on this group of deepsea fishes, for identification.

Even before I had taken it out of the jar, I recognized the fish as a *Lepidorhynchus denticulatus*, a species originally described by Sir John Richardson in 1846 from a dried specimen that "was thrown up on the beach of South Australia, and has lost part of its tail" (Richardson 1846:54). Despite the desiccated state of the type specimen, the original description and illustration more than adequately characterized this distinctive grenadier, which is the sole representative of the genus.

The species was previously known only from the coasts of south and southeastern Australia and off the coasts of New Zealand in depths ranging from less than 100 m to more than 1000 m. It is one of the most common grenadier in these waters and forms a significant part of the by-catch of trawlers fishing at upper-slope depths. So far as known, the species has not been recorded north of latitude 34°S off New Zealand and about 30°S off southeastern Australia. Its distribution is generally confined to subtropical waters. Its occurrence off Hawaii is thus most astounding and prompts the recording of this extraordinary specimen.

METHODS

Methods for making counts and measurements follow Iwamoto and Sazonov (1988). Institutional abbreviations follow Leviton et al. (1985).

Description

Lepidorhynchus denticulatus Richardson, 1846

Figs. 1–2

Macrourus vel *Lepidorhynchus denticulatus* Richardson, 1846:1–2, pl. 32, fig. 1–3 (holotype: BMNH 1845.11.31.6; type locality: coast of South Australia).
Coryphaenoides denticulatus: Günther, 1862:396.
Macrurus (*Optonurus*) *denticulatus*: Günther, 1887:147.
Optonurus denticulatus: Gilbert and Hubbs, 1916:144.
Lepidorhynchus denticulatus: Phillipps, 1927:58.

MATERIAL EXAMINED.— BPBM 39286 (200 mm total length, tail complete; sex indeterminate); Hawaii, Oahu, northwest side about 2 miles (3.2 km) offshore; collected by Richard Cadaoas, 16 August 2004 from stomach of 18–20-inch (46–51 cm) squid caught by hook and line at night. CAS 220920 (6 spec., 240+–456 mm total length); Australia; New South Wales, off Bermagui; 36°46′–41'S, 150°21′E; 285–310 fm [521–567 m]; collected by Ken Graham on F/V "Shelley," by trawl; 15 February 2000.

COUNTS AND MEASUREMENTS.— (Hawaiian specimen first, followed by range of Australian specimens in parentheses.) First dorsal-fin rays II,11 (10–12); pectoral-fin rays i17 and i16 (i15–i18); pelvic fin rays 9 (9); branchiostegal rays 6; gill rakers first arch (outer/inner) 0+11 / 3+13 (0+10–14 / 3–4+13–15 = 17–18), second arch 3+14 / 2+13 (2–3+12–15 = 14–17 / 2–3+12–14 = 14–17); scale rows below origin of first dorsal fin about 8 (about 7–8), below mid-base of first dorsal fin about 5 (5.5), below origin of second dorsal fin about 6 (5–6.5); pyloric caeca 16 (15–25). Head length 31.5 mm (41.7–70.3 mm); the following in mm for Hawaiian specimen followed in parentheses by percent of head length for Hawaiian specimen and then Australian specimens: snout length 7.6 (22%, 20–24%); preoral length 5.1 (16%, 9–13%); internasal width 6.8 (22%, 16–21%); interorbital width 8.8 (28%, 20–25%); orbit diameter 12.6 (40%, 35–39%); suborbital width 2.8 (9%, 8–8%); postorbital length 12.6 (40%, 41–45%); distance orbit to angle of preopercle 11.9 (38%, 39–42%); length upper jaw 15.3 (49%, 47–50%); length barbel 3.1 (10%, 9–15%); length

FIGURE 1. *Lepidorhynchus denticulatus*, BPBM 39286 (31.5 mm head length, 200 mm total length), from off Oahu, Hawaii.

outer gill slit 8.6 (27%, 22–27%); preanal length 47.5 (151%, 158–177%); distance outer pelvic fin to anal-fin origin 17.7 (56%, 53–69%); distance isthmus to anal-fin origin 32 (102%, 108–139%); greatest body depth 24.5 (78%, 79–90%); body depth at anal-fin origin 20.0 (63%, 64–80%); interspace between first and second dorsal fins 23.5 (75%, 74–95%); height first dorsal fin 28.5 (90%, 78+–92); length base of first dorsal fin 11.1 (35%, 34–42%); length pectoral fin 23 (73%, 72–82%); length outer pelvic-fin ray 20.5 (65%, 57–62%).

General description of Hawaiian specimen, with condition in larger Australian specimens in parentheses, if different. Body long and slender, laterally compressed, tapering posteriorly from abdomen into a long tail that ends in a fine point. Width of body across pectoral-fin bases less than half body depth below origin of first dorsal fin; greatest depth about equal to distance from anterior margin of orbit to end of opercle. Head about 6.2 into total length, compressed, its greatest width slightly greater than orbit diameter. Snout rounded and narrow, its tip slightly behind vertical of tip of jaws (slightly forward in larger Australian specimens). Orbits huge, more than postorbital length (slightly less than postorbital), about 2.4 into head length; its dorsal margin entering dorsal profile of head. Mouth large, essentially terminal, unrestricted by lip folds at angle; posterior margin of premaxillary approximately below middle of orbit (below posterior margin of pupil). Suborbital region narrow, shelf and ridge well defined, although this may be partly caused by slightly desiccated state of specimen. Preopercle broadly rounded, its ridges well defined, covering most of interopercle (except anteroventrally and distal tip) and anterior part of subopercle, which ends ventrally in a short tab. Chin barbel short, fine, its length about equal to diameter of posterior nostril. Gular membrane narrowly connected at isthmus far forward under middle of orbit (posterior half of orbit), overlapping and forming a deep fold over branchiostegal membrane. Anus immediately in front of anal-fin origin, separated at most by one or two scale rows. Swimbladder large, elongated, with eight or nine broad, flat retia, each connected to a globular to elongated bean-shaped gas gland (Fig. 2).

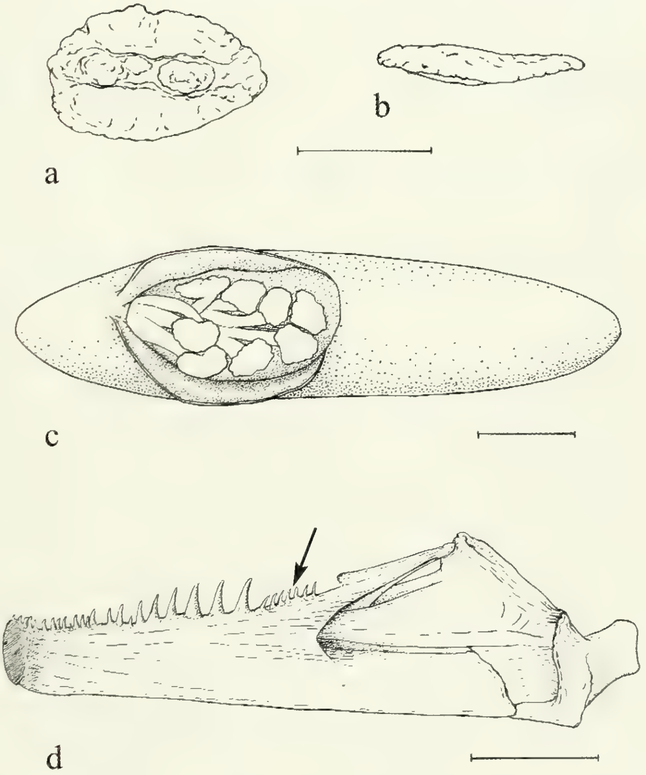

FIGURE 2. *Lepidorhynchus denticulatus*, CAS 202920, 41.7 mm head length, 240+ mm total length. Saggital otolith, (a) mesial and (b) dorsal views; (c) swimbladder, showing retia and gas glands; (d) mesial view of lower jaw showing comblike teeth (arrow).

Teeth on premaxilla in moderately wide band extending entire length of jaw opening; teeth small and conical or spikelike, except outer series of much larger, widely spaced canines in a single row. Dentary teeth small anteriorly and in one or two irregular series, becoming increasingly larger posteriorly and in a single file. Larger teeth end abruptly and followed at posterior angle of jaws by a series of seven (four or five) comb-like teeth, slightly reclined, closely set, and somewhat overlapping at bases. These comblike teeth unlike those seen in any other grenadier. (In much larger Australian specimens, these teeth fewer and mostly embedded in gum tissue.) As with all other macrouroid fishes, no teeth on vomer and palatines.

First dorsal fin high, triangular, with two spinous rays and 11 segmented rays, anteriormost segmented rays appear to be longest. First spinous ray short and splintlike, tightly coalesced with proximal part of long second spinous ray. Distally on second spine a few small thornlike denticles on leading edge (absent in larger Australian specimens). Interspace between first and second dorsal fins wide, much greater than length base of first dorsal fin. Rays of second dorsal fin low and fine to end of tail, although gradually increasing in height posteriorly. Anal fin well developed throughout, its origin slightly behind vertical through posterior edge of first dorsal fin. Upper edge of pectoral fin about at mid-lateral line; fin well developed, relatively long, its length about equal to postrostral length of head, its tip extending to above 10th (4th or 5th) anal ray. Pelvic fins well developed; distal tip of outermost ray filamentous and hairlike, just reaching anal-fin origin.

Luminescent tissue on ventral surfaces of body extensive and consisting of extremely fine transverse parallel black lines, the ventral striae. Luminescent tissue extends from isthmus over abdomen up to and slightly behind pectoral-fin base (as well as lateral surface of fin base), narrowing posteriorly to above anus, gradually tapering above anal fin to approximately 57th (53–57) anal-fin ray. Tissue readily observed in preserved specimens as black areas underlain by extremely fine parallel black lines; in fresh specimens, these areas of striae usually overlain by a silvery reflection and striae much less apparent. (Ventral striae are also found in several unrelated groups such as the cardinalfishes of the genus *Siphamia* [Apogonidae], and the berycoids *Aulotrachichthys* spp. and *Paratrachichthys* spp. [Trachichthyidae]). A small, flat, black, triangular light organ situated within median line of abdominal wall closely adherent to base of rectum. Light organ externally manifested as a round white or translucent body encircled by a narrow black ring continuous with anal surround.

Body scales of moderate size throughout, somewhat deciduous, and fully covered with fine, conical, needle-like spinules arranged in more or less parallel rows. (In larger Australian specimens, 30 or more rows of spinules on scales below interspace between dorsal fins.) Body scales almost entirely missing in Hawaiian specimen, but a few remain on nape and top of head. (Scales cover most of head, although lower surface of snout naked. Tiny scales incompletely cover suborbital region.) Mandibular rami fully scaled. Gular and branchiostegal membranes naked. (Australian specimens have lowermost branchiostegal rays scaled, and in one specimen, exposed anteroventral margin of interopercle densely covered with tiny oval scales, each having a few short, upright spinules.) None of scales on head enlarged or thickened.

Color in alcohol of denuded Hawaiian specimen overall flesh colored with prominent black areas corresponding to luminescent tissue. Gill membranes, lower parts of head, and opercle posterior to preopercular ridge blackish. Fins clear, although first dorsal fin somewhat light dusky. (In fresh specimens, species silvery over most lateral surfaces of head and body, with dorsum gray and area over luminescent tissue black. Pelvic fins blackish; pectoral fins light dusky.)

Comparisons

The small size of the Hawaiian specimen made comparison of the morphometry of head and body structures uncertain. Several proportions of head parts in BPBM 39286 were greater than in the larger Australian specimens: snout length, preoral length, internasal width, interorbital width, orbit diameter, and suborbital width. The postorbital and orbit-to-preopercle measurements were slightly lower, but those were probably related to the relatively larger orbit diameter, which typically shows allometric growth in grenadiers. That the interorbital and suborbital widths were not narrower is somewhat contrary to what one would expect. The slightly lower values for the preanal length, the distance of isthmus to anal-fin origin, and the greatest body depth are not uncommon in smaller individuals of grenadier species. The weakly and sparsely denticulated distal portion of the spinous dorsal ray is also seen in the smallest Australian specimen and depicted in the original illustration of the holotype. In the larger Australian specimens, these denticulations are lost. All other characters appear exactly the same in Hawaiian and Australian specimens, and despite the small differences in some head proportions, there is little reason to doubt the conspecificity of the two populations at this time. The possibility of there being two species cannot be completely discounted, however, and a more-definitive conclusion can only be made after additional specimens from Hawaii become available.

DISCUSSION

The unusual Hawaiian record of this species leads to speculation as to how this particular individual found its way so far across the Pacific from its normal grounds some 3700 nautical miles and more than 54 degrees of latitude distant. Many species of grenadiers have broad distributions, but those can generally be separated into three categories: (1) abyssal or lower-slope species, such as *Coryphaenoides armatus* (Hector, 1875) and *Cetonurus* spp.; (2) bathypelagic species, such as *Cynomacrurus piriei* Dollo, 1900 and *Odontomacrurus murrayi* Norman, 1939; and (3) species having a long-lived pelagic juvenile stage, the prime example being *Malacocephalus laevis* Lowe, 1843. *Lepidorhynchus denticulatus* does not appear to fit into any of these categories (but its early life history is not known), so its presence in the Hawaiian Islands is a mystery. Were it to be found in intervening areas of the western Pacific, its presence in Hawaiian waters would not be so surprising. Yet, despite relatively extensive collecting at appropriate depths throughout the central and North Pacific, especially by Japanese vessels, *L. denticulatus* has yet to be recorded north of New Zealand and southeastern Australia. Extensive trawling on the Lord Howe Rise and Norfolk Ridge north of New Zealand during the cooperative (New Zealand and Australia) NORFANZ cruise of the R/V *Tangaroa* in 2003 captured the species only once, and that was west of Three Kings Islands off the northern tip of New Zealand's North Island at 34°S. The extensive French survey cruises to New Caledonia and adjacent areas failed to produce any specimen of the species.

Most species of grenadiers are localized in their distributions, usually to basins, island groups, oceanic seamounts and ridges, or along continental margins that are bounded by differing oceanographic or geologic conditions. So far as known, besides *Lepidorhynchus denticulatus*, only five species of grenadiers from Hawaii are also known from Australia or New Zealand: *Malacocephalus laevis, Kuronezumia bubonis* (Iwamoto, 1974), *Hymenocephalus aterrimus* Gilbert, 1905, *Nezumia propinqua* (Gilbert and Cramer, 1897), and *Trachonurus sentipellis* (Gilbert and Cramer, 1897). The last three are found in Australian waters but not off the coasts of New Zealand's main islands. *Malacocephalus laevis* and *K. bubonis* are widespread throughout most of the Pacific, Atlantic and Indian oceans, and *N. propinqua* is widespread in the Pacific and Indian oceans, although there is some question as to whether that name is currently being applied to more than one species. *Trachonurus sentipellis* is recorded from Hawaii, the New Caledonian region, and Australia, but there is again some doubt that the Hawaiian populations are the same species as the austral populations. If the identifications are correct, this species comes closest in its distribution to that of *Lepidorhynchus.*

It has been theorized (Marshall 1965, 1973) that most grenadiers have pelagic eggs that hatch near the bottom; the larval stage is very short before metamorphosis into a pelagic juvenile stage (sometimes called postlarva or prejuvenile) takes place. The young probably spend relatively little time in the midwaters before descending to the bottom to live a benthopelagic life. A short pelagic early life would ensure that the settled young are over appropriate living depths and are not wafted too far from the narrow continental slopes on which adult populations live. The scarcity of larval grenadiers in collections, despite the group's abundance throughout the world's oceans, adds support to this idea of a short pelagic stage lived close to the bottom. Perhaps there are some species that can tolerate an extended pelagic larval or juvenile stage when wafted far beyond their normal range. The concept of "expatriate" individuals is well known for some fishes, and this may come into play with some unusual range extensions in grenadiers. Whether any of these factors may account for the extraordinary occurrence of *L. denticulatus* in Hawaii is yet to be learned, as the early life history of the species is not known, nor is it known that *L. denticulatus* is actually established in the Hawaiian Islands. It seems unlikely, however, that the captured specimen represents a single stray individual in these waters.

There are few examples of other demersal shelf and upper-slope fishes of southern Australia and New Zealand that have a distribution also in the Hawaiian Islands. Mr. Suzumoto informs me (in litt., Nov. 2004) that the Bishop Museum has "a specimen of *Cheilidonichthys kumu*" caught off Hawaii Island in 1926 and never seen here since." That Bishop Museum sea robin (family Triglidae) was recorded by Pietschmann (1930) and considered of questionable validity by Springer (1982:103). It was said (Gomon et al. 1994:496) to occur off South Africa, southern Australia, and New Zealand, and also in the North Pacific off Japan, Korea, and China; however, recently published books on the Japanese fish fauna (e.g., Masuda et al. 1984; Nakabo 2002) list *C. spinosus* and *C. ischyrus* but not *C. kumu*. Martin F. Gomon (NMV) has informed me (*in litt.*, 12 Dec. 2004) that Peter Last (of CSIRO) "has differentiated several species of *Cheilidonichthys* in Australia, probably none of them also in South Africa, and the Japanese species are probably something else again." Gomon adds that "there are other Hawaiian cognates, like the *Bodianus oxycephalus*-like species. . .with 3 cognates in Japan, southern Pacific and SW Australia, respectively." The morwong *Cheilodactylus vittatus* was thought to have a north-south disjunct distribution: the Hawaiian Islands in the northern hemisphere, the Lord Howe Island and New Caledonia in the southern hemisphere (Springer 1982:33). Burridge (2004), however, has reported that the New Caledonia and Norfolk Island *Cheilodactylus* represents a different species, which he described as *C. francisci*. The mirror dory, *Zenopsis nebulosus*, is a wide-ranging shelf to upper-slope species (62–550 m) found off Australia, New Zealand and Chile in the southern hemisphere, and also in the North Pacific off Japan, Korea, Hawaii and California (Gomon et al. 1994:420–421). Of the three deep-dwelling (100–400 m) Emmelichthyidae in Hawaii, one species also occurs off Japan, Australia and the Philippines (Springer 1982:41). In light of these few examples, it is apparent that many fish species formerly thought to have a broadly disjunct distribution in Hawaii and the southwest Pacific are, in fact, separable into more than one closely related species. Other examples are likely to surface after closer study using tools and knowledge not formerly available. That possibility for *Lepidorhynchus* cannot at this time be discounted.

Springer (1982:117), in his valuable study on Pacific Plate biogeography, found 121 families of shorefishes that are nonmarginally represented on the Pacific Plate. Of these, 15 families (12%) are found only in the Hawaiian Islands, and 10 of the 15 occur there only in deep water. These "Hawaiian exceptions," as so designated by Springer, "denote Indo-Pacific taxa that occur nonmarginally on the Pacific Plate only at the Hawaiian Islands. These taxa usually occur also in Japan and/or the Ruykyu [*sic*; misspelling for Ryukyu] Islands, and many are antitropically distributed in the Indo-West Pacific; some are restricted to north of the tropics and some are moderately deep dwelling." (Springer 1982:135.). *Lepidorhynchus* should be added as an Hawaiian exception, but the underlying cause of its apparent disjunct distribution is unknown.

Central to understanding the vicariant event that produced the current distribution of *Lepidorhynchus*, one should have a firm grasp of its closest relatives. "If one knows the cladistically determined closest relatives (sister groups) of endemic taxa, and the distributions of those relatives, one can narrow the geographic and temporal search for the pertinent vicariant events." (Springer 1982:6). Unfortunately, the sister-group relationships of *Lepidorhynchus* within the Macrouridae are uncertain and a thorough cladistic analysis of macrourid genera has yet to be made. Iwamoto and Sazonov (1988:39), in their tentative phylogeny of macrourines with six branchiostegal rays, included the genera *Cynomacrurus* and *Odontomacrurus* in a clade, with *Lepidorhynchus* as the clade's questionable sister group. *Odontomacrurus murrayi* perhaps comes closest in overall morphology to *Lepidorhynchus*, having a compressed head, large, terminal jaws beset with canines, and a small light organ. That bathypelagic species, however, lacks ventral striae, a developed swimbladder, and a chin barbel, and it has many reductions and differences in its morphology and organ systems that reflect its bathypelagic existence and thereby distance it from *L. denticulatus*. The broad, almost worldwide distribution of *O. murrayi* in tropical to subtropical waters shows a noteworthy hiatus — so far as known, there are no records of its presence on the Pacific Plate except marginally.

Of the grenadiers with seven branchiostegal rays, the luminescence on the body, the rounded snout with little protrusion of the rostrum, and the scale spinulation are most suggestive of *Hymenocephalus,* but the six branchiostegal rays, the eight or nine retia and gas glands, the absence of a light organ lens on the chest, the very different dentition, and the narrowly compressed head in *Lepidohynchus* are among several characters that separate it from members of *Hymenocephalus*. The head shape, especially the narrow snout with little protrusion of the median nasal ridge, is somewhat like that of *Ventrifossa atherodon* (Gilbert and Cramer, 1897) and the scale morphology is quite similar, but members of *Ventrifossa* lack ventral striae, they have seven branchiostegal rays and two retia and gas glands, and there is a small dermal window of the light organ between the pelvic-fin bases that is absent in *Lepidorhynchus*. *Steindachneria argentea* Goode and Bean, 1886, in the monotypic family Steindachneriidae, bears some resemblance to *L. denticulatus* in its ventral striae, large terminal mouth beset with canine-like teeth, and similar retia and gas glands in the swimbladder (see Marshall 1966, fig. 3C), but differs radically in having second dorsal rays well developed and higher than most anal-fin rays, an elevated lobe in the otherwise low anal fin, vomerine teeth, no chin barbel, anus located between pelvic-fin bases and distantly separated from urogenital opening, which is immediately before the anal fin. It is apparent that a more thorough comparative study of the morphology of *Lepidorhynchus denticulatus,* perhaps combined with molecular investigations, will be needed to clarify the phylogenetic position and discover the sister group of this perplexing species.

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The Phylogenetic Position of the Recently Rediscovered Philippine Forest Turtle (Bataguridae: *Heosemys leytensis*)

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The Philippine forest turtle (*Heosemys leytensis*) is one of the least-known Asian turtles. Until recently it was only known from a single specimen, the neotype (CAS 60930). The rediscovery of this enigmatic turtle in the wild provides access to fresh genetic material, allowing us to rigorously test its phylogenetic position among Asian pond and wood turtles of the clade Bataguridae for the first time. We sequenced 1174 bp of mitochondrial DNA (cyt*b*) and 1076 bp of nuclear DNA (R35 intron) from a newly acquired specimen of *H. leytensis* (PNM 8488) and compared our sequences to a previously published genetic survey of batagurids. Our main goal is to determine if *H. leytensis* is closely related to other species of *Heosemys* (*H. spinosa* [type species], *H. grandis, H. depressa*, and *H. annandalii* [comb. nov.]). Parsimony and likelihood analyses of mitochondrial and nuclear DNA data strongly support *H. leytensis* as the sister taxon to the Southeast Asian species *Siebenrockiella crassicollis* (commonly known as the 'black marsh turtle' or 'smiling terrapin'). The close relationship between *H. leytensis* and *S. crassicollis* is a novel hypothesis, although both share an easily recognizable diagnostic feature: vertebrals 2–4 are mushroom-shaped or 'ginkgo leaf'-shaped. In order to eliminate two potentially monotypic genera, the genus *Siebenrockiella* is phylogenetically defined to accommodate the close relationship between* *S. crassicolis* **and *H. leytensis* **whereas a new name, *Panyaenemys*, is defined for the distinct *H. leytensis* stem lineage.**

The rediscovery of wild populations of the Philippine forest turtle (*Heosemys leytensis* Taylor 1920; Fig. 1B-E) in the Palawan island group of the western Philippines (Fig. 1A; Diesmos et al. 2004a), resolved a decades-long search for this species. Prior to this, our knowledge of *H. leytensis* was restricted to the original published description (the type series was lost in the destruction of the Bureau of Science, predecessor to the National Museum of the Philippines, during World War II; Brown and Alcala 1978; Buskirk 1989), one museum specimen (CAS 60930, the neotype, Fig. 1B,C) reported by Buskirk (1989), and one specimen from Palawan (UF/FSM 67515) reported by Timmerman and Auth (1988). Thus, for over forty years, no museum specimens of *H. leyten-*

sis were known and so it remained one of the least-known Asian turtles.

The rediscovery of *H. leytensis* in the wild (Diesmos et al. 2004a) provides access to fresh genetic material, allowing us to rigorously test its phylogenetic position within the 'Asian pond and wood turtles' (Bataguridae Gray, 1870 = 'Geoemydidae Theobald, 1868'; Joyce et al. 2004) for the first time. Batagurids are a species-rich group (60+ spp.) of highly threatened (van Dijk et al. 2000), but poorly studied non-marine turtles from Asia. A taxonomic reassessment of *H. leytensis* is necessary because the content and diagnosis of batagurid genera have changed dramatically since Taylor (1920) described the Philippine forest turtle as *Heosemys leytensis* (e.g., Ernst and Barbour 1989; Iverson 1992). The twelve characters that Taylor (1920) used to diagnose *Heosemys* are now known to be either plesiomorphic for batagurids or else appear in other genera as homoplasy (Joyce and Bell 2004). One of these characters, the derived absence of a temporal arch in the skull, has played a particularly important role in maintaining *H. leytensis* in the genus *Heosemys*. Besides being noted by Taylor (1920), this character was later used by McDowell (1964) to diagnose *Heosemys* (including *H. leytensis*) and was also described in the *H. leytensis* neotype (Buskirk 1989). This character is also known in *Hieremys annandalii* (Boulenger, 1903) as well as some species of testudinoid box turtles from China and North America (*Cuora* Gray, 1855 and *Terrapene* Merrem, 1820; Zangerl 1948; McDowell 1964; Joyce and Bell 2004). Because *H. leytensis* lacks the characteristic hinged plastron of a box turtle, its referral to *Heosemys* seems logical.

Although *H. leytensis* shares the absence of the temporal arch with other *Heosemys*, it is morphologically divergent from other *Heosemys* in other respects. For example, *H. leytensis* usually has mushroom-shaped or 'ginkgo leaf'-shaped vertebral scales 2–4 (Fig. 1B, E), a feature that is otherwise restricted to the 'smiling terrapin' of southeast Asia, *Siebenrockiella crassicollis* (Gray 1831) (Fig. 1F–G). Additionally, the projecting gular region (anterior region of the plastron) of *H. leytensis* clearly distinguishes it from all other batagurid lineages, including other species referred to *Heosemys*. In this character, it superficially resembles some species of terrestrial tortoises (Testudinidae Gray, 1825), the sister-taxon to batagurids (Spinks et al. 2004).

Given the extensive homoplasy within batagurid morphology (Joyce and Bell 2004) and the overall distinctiveness of *H. leytensis*, it is difficult to confidently place *H. leytensis* into any existing genus on morphological grounds alone. Moreover, weak nodes generated from cladistic analyses of morphological variation in Bataguridae (Hirayama 1985; McCord et al. 1995) are strongly rejected by molecular studies (McCord et al. 2000; Spinks et al. 2004). For this reason, we tested the phylogenetic position of *H. leytensis* with cladistic analyses of mitochondrial and nuclear DNA sequences.

Our primary goal was to determine whether *H. leytensis* should continue to be recognized as a member of the genus *Heosemys*. But in order to avoid confusion, we must establish an explicit concept of *Heosemys* and what species names this informal clade name should include. Spinks et al. (2004) reported DNA sequences from three species of *Heosemys* including one sample attributed to the type species *Heosemys spinosa* (Gray, 1831). According to their study, *Heosemys* form a well-supported clade with *Hieremys annandalii*, and so Spinks et al. (2004) raised the possibility that *H. annandalii* might be better placed within an expanded *Heosemys*. However, Spinks et al. (2004) refrained from making a taxonomic change pending future evidence for the possible placement of *Hieremys annandalii* relative to *Heosemys* species. We think this reticence is unwarranted inasmuch as *Hieremys* Smith, 1916 is a monotypic genus and *H. annandalii* forms a well-supported clade with other *Heosemys*. The Spinks et al. (2004) suggestion to expand the older genus name (*Heosemys*) to the well-supported node creates a much more stable taxonomy. Under this scheme, the widely-used genus name will remain stable regardless of the ultimate resolution of the position within the *Heosemys* basal polytomy. We refer *Hieremys annandalii* to the genus *Heosemys*, but

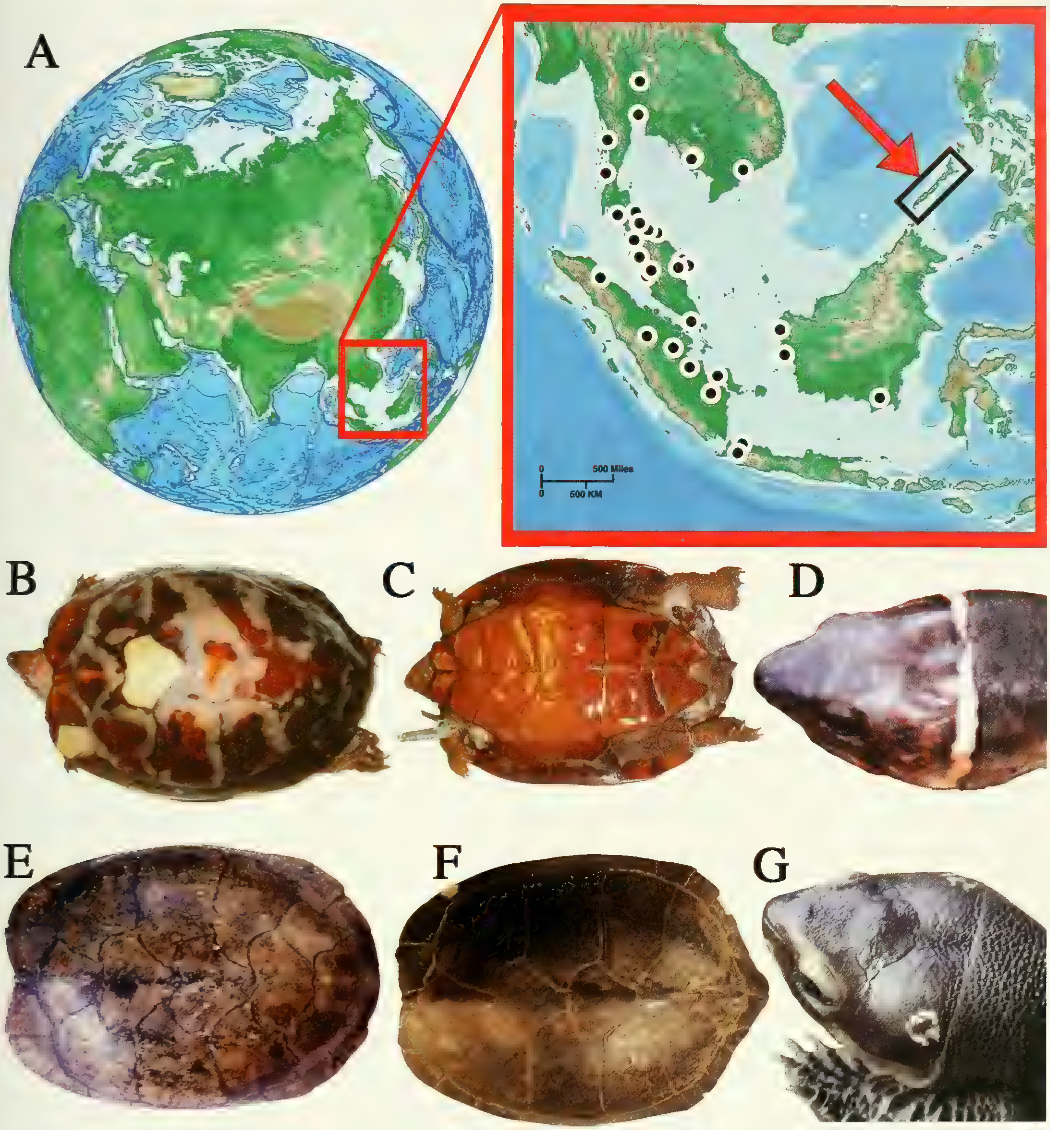


FIGURE 1. A: Map showing the known distribution of *Siebenrockiella crassicollis* (dots) based on Iverson (1992) and Stuart and Platt (2004). The black rectangle includes the known and hypothesized range of *Heosemys leytensis* based on Diesmos et al. (2004b); B-C: Neotype specimen of *Heosemys leytensis* (CAS 60930), dorsal [note the missing 'ginkgo leaf'-shaped vertebral 2] (B) and ventral view (C); D: Dorsal view of *H. leytensis* head showing diagnostic markings; E: Dorsal view of *H. leytensis* possibly from Dumaran Island (see Diesmos et al., 2004a); F: Dorsal view of *S. crassicollis* (FMNH 224070); G: View of *S. crassicollis* head showing the diagnostic markings.

refrain from defining the genus *Heosemys* phylogenetically until we discuss our results, especially regarding the placement of *H. leytensis*. In summary, our concept of *Heosemys* is the clade that includes the type species *Heosemys spinosa*, the aforementioned *Heosemys* [orig. *Cyclemys*] *annandalii* (Boulenger, 1903) comb. nov., *Heosemys grandis* (Gray, 1860), and *Heosemys depressa* (Anderson, 1875).

INSTITUTIONAL ABBREVIATIONS.— CAS, The California Academy of Sciences, San Francisco, California, USA; FMNH, The Field Museum of Natural History, Chicago, Illinois, USA; PNM, National Museum of the Philippines, Manila, Philippines; UF, Florida Museum of Natural History, University of Florida, Gainesville, Florida.

MATERIALS AND METHODS

Ethanol-preserved muscle was taken from a museum specimen of *Heosemys leytensis* (PNM 8488, see Material Examined). Total genomic DNA was extracted from the muscle using PureGene Animal Tissue DNA Isolation Protocol (Gentra Systems, Inc.). Primers for amplifying and sequencing parts of cyt*b* and tRNA-Thr (collectively 'cyt*b*') were taken from Spinks et al. (2004) and R35 primers were taken from Fujita et al. (2004). PCR products were electrophoresed in a 1% low melt agarose TALE gel stained with ethidium bromide and visualized under ultraviolet light. The bands containing DNA were excised and agarose was digested from bands using GELase (Epicentre Technologies). PCR products were sequenced in both directions by direct double-strand cycle sequencing using Big Dye version 3.1 chemistry (Perkin Elmer). Cycle-sequencing products were precipitated with ethanol, 3 M sodium acetate, and 125 mM EDTA, and sequenced with a 3730 DNA Analyzer (ABI). Sequences were edited and protein-coding regions were translated into amino acids with Sequencher version 4.1 (Genecodes).

We compared new cyt*b* and R35 sequences with the sequences reported by Spinks et al. (2004). Sequences were aligned by eye into the matrix used by Spinks et al. (2004) and deposited into TreeBASE (www.treebase.org, accession number S1002). Our sequences (cyt*b*, 1174 bp; R35, 1076 and 1078 bp) were longer than those used in the Spinks et al. (2004) alignment; the extra base pairs were excluded from the analysis. For the parsimony analysis of combined data sets, we included 72 of the 79 taxa sequenced by Spinks et al. (2004), excluding seven putative hybrids. Some of these hybrids were described as new species from pet trade samples leading to taxonomic confusion that is not yet fully resolved (Parham et al. 2001; Wink et al. 2001; Spinks et al. 2004). We avoid these issues by removing the suspect taxa from consideration. We feel that we are justified in doing this because an initial phylogenetic analysis (not shown) demonstrated that *H. leytensis* is not closely related to any of these taxa and the inclusion or exclusion of these sequences does not affect the phylogenetic position of *H. leytensis*. Besides *H. leytensis*, the only addition to the Spinks et al. (2004) data set was the sequence of one vouchered *Siebenrockiella crassicollis* sample from Cambodia (see below).

In addition to the aforementioned combined analysis, we analyzed the mitochondrial and nuclear data sets separately in order to compare the potential congruence or conflict in the phylogenetic signal of our markers. We also performed a maximum likelihood and Bayesian analyses on a restricted data set that includes 28 of the 79 species from Spinks et al. (2004). These 28 sequences represent all the non-hybrid taxa from the Spinks et al. (2004) study that have both cyt*b* and R35 sequenced. The restricted data set is still appropriate for placing *H. leytensis* because it contains every major lineage (i.e., genus) of batagurid.

Parsimony analyses were performed using the 1000 random addition-sequence replicates of the heuristic search algorithm in PAUP*4.0b10 (Swofford 2002). Support for the parsimony analyses was determined using bootstrap and decay indices. For the combined analysis, we used 1000 bootstrap replicates with 10 random addition-sequence replicates each. Decay indices were calculated using a PAUP command file generated by MacClade 4.0 (Maddison and Maddison 2000). For the likelihood analyses, we used hierarchical likelihood-ratio tests with ModelTest (Posada and Crandall 1998) to determine which model was appropriate. For the standard likelihood analysis the model GTR+I+G was selected, with proportion of invariable sites 0.3836, gamma distribution shape parameter 0.4762, and base frequencies as A=0.3198, C=0.3039, G=0.1336, and T=0.2427. Maximum likelihood analyses were performed with 100 random addition replicates with stepwise addition of taxa using the heuristic search algorithm and TBR branch swapping. For the Bayesian analysis, we separated the cyt*b* and R35 data into their own partitions and estimated the best models for each (GTR+I+G and HKY respectively). Using these parameters, we performed three mixed-model analyses of five million generations and four chains each using MrBayes v3.0b4 (Huelsenbeck and Ronquist 2001). We plotted the log likelihood scores against generation to determine when the analysis achieved stationarity for each analysis. In each case, the seven thousand trees recovered prior to stationarity were discarded as 'burn in' and a 50% majority rule consensus was used to determine the posterior probabilities for each clade.

RESULTS

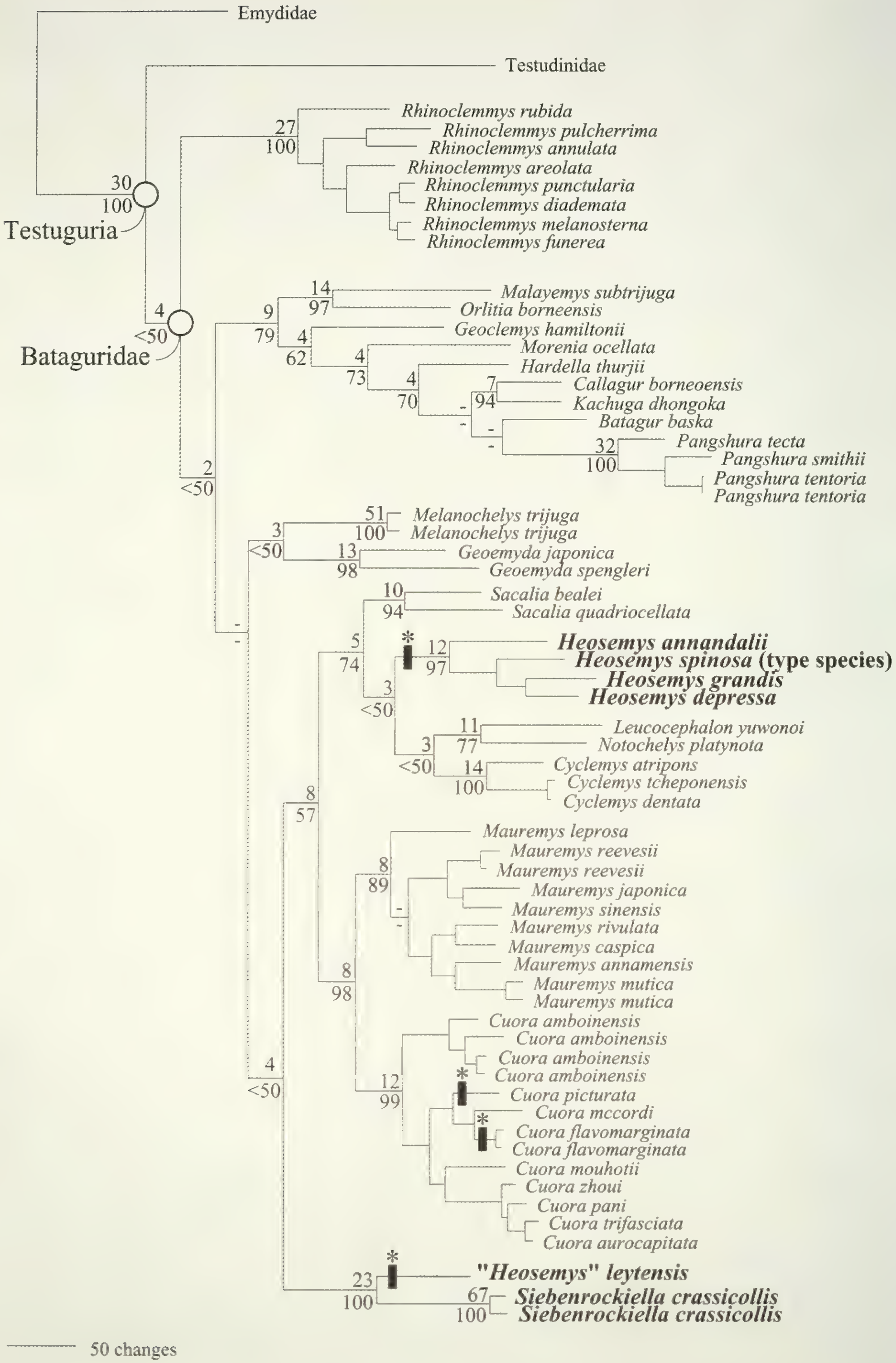
In our initial analyses, the sequence from our sample of *H. leytensis* is consistently placed as the sister taxon to *S. crassicollis* with high statistical support. None of the samples from the Spinks et al. (2004) study have vouchered specimens, so we confirmed our initial results by sequencing a vouchered specimen of *S. crassicollis* from Cambodia (see Material Examined). All tree statistics were calculated with the additional sample included. All analyses (parsimony, likelihood, Bayesian) place *H. leytensis* and *S. crassicollis* as sister taxa (Fig. 2). In the parsimony and Bayesian analyses, *H. leytensis* and *S. crassicollis* are united with high statistical support (100% parsimony bootstrap, 23 decay index, 100% Bayesian posterior probability). Parsimony analyses of the separate cyt*b* and R35 data sets (not shown) show that the *H. leytensis* + *S. crassicollis* clade is independently supported by our mitochondrial and nuclear markers. Meanwhile, the other species of the genus *Heosemys* form a well-supported clade that is separated from *H. leytensis* + *S. crassicollis* clade by several branches (Fig. 2).

DISCUSSION

Our study demonstrates that the continued placement of *H. leytensis* in the genus *Heosemys* is no longer tenable. Inasmuch as the other species of *Heosemys* form a well-supported clade, which is readily-diagnosable with molecular and morphological data, we phylogenetically define the genus *Heosemys* as the crown clade arising from the last common ancestor of *Heosemys* [orig. *Emys*] *spinosa* (Gray, 1831), *Heosemys* [orig. *Geoemyda*] *grandis* (Gray, 1860), *Heosemys* [orig. *Geoemyda*] *depressa* (Anderson, 1875), and *Heosemys* [orig. *Cyclemys*] *annandalii* (Boulenger, 1903).

The hypothesis that *H. leytensis* and *S. crassicollis* are sister taxa within Bataguridae is a novel result. Both *H. leytensis* and *S. crassicollis* share two diagnostic characters that may have been inherited from a common ancestor: 1) Vertebrals 2–4 are 'ginkgo leaf'-shaped. *Orlitia borneensis* Gray 1873 has a superficially similar condition, but it is restricted to the first vertebral; 2) Light spots or lines in the posterior dorsal region of the head. In *S. crassicollis* (Fig. 1G), this character occurs as two circles or spots that may fade with age (Lim and Das 1999) whereas in *H. leytensis* (1C) it is a straight line that is faint or absent in 35% of individuals (Diesmos et al. 2004a, b). A similar, but more dramatic, condition of posterior head marking occurs in parallel in the 'eyed turtles' of the genus *Sacalia* Gray 1870.

Additional morphological comparisons of *S. crassicollis* and *H. leytensis*, including skeletal material, may reveal more potential synapomorphies. Meanwhile, the character that has long been used to place *H. leytensis* in the genus *Heosemys*, the absence of a complete temporal arch, is more


Emydidae
Testudinidae
Rhinoclemmys rubida
27
100
Rhinoclemmys pulcherrima
Rhinoclemmys annulata
Rhinoclemmys areolata
Rhinoclemmys punctularia
Rhinoclemmys diademata
Rhinoclemmys melanosterna
Rhinoclemmys funerea
30
100
Testuguria
14
97
Malayemys subtrijuga
Orlitia borneensis
9
79
4
62
Geoclemys hamiltonii
4
<50
Bataguridae
4
73
Morenia ocellata
Hardella thurjii
4
70
7
94
Callagur borneoensis
Kachuga dhongoka
Batagur baska
32
100
Pangshura tecta
Pangshura smithii
Pangshura tentoria
Pangshura tentoria
2
<50
51
100
Melanochelys trijuga
Melanochelys trijuga
3
<50
13
98
Geoemyda japonica
Geoemyda spengleri
10
94
Sacalia bealei
Sacalia quadriocellata
5
74
*
12
97
Heosemys annandalii
Heosemys spinosa (type species)
Heosemys grandis
Heosemys depressa
3
<50
11
77
Leucocephalon yuwonoi
Notochelys platynota
3
<50
14
100
Cyclemys atripons
Cyclemys tcheponensis
Cyclemys dentata
8
57
Mauremys leprosa
8
89
Mauremys reevesii
Mauremys reevesii
Mauremys japonica
Mauremys sinensis
Mauremys rivulata
Mauremys caspica
Mauremys annamensis
Mauremys mutica
Mauremys mutica
8
98
Cuora amboinensis
Cuora amboinensis
Cuora amboinensis
Cuora amboinensis
4
<50
12
99
*
Cuora picturata
Cuora mccordi
*
Cuora flavomarginata
Cuora flavomarginata
Cuora mouhotii
Cuora zhoui
Cuora pani
Cuora trifasciata
Cuora aurocapitata
*
23
100
"Heosemys" leytensis
67
100
Siebenrockiella crassicollis
Siebenrockiella crassicollis
50 changes

homoplastic than previously thought. If this character is optimized onto the phylogeny (Fig. 2), it predicts that the temporal arch was lost at least three independent times within Bataguridae: once in the *H. leytensis* stem-lineage, once in the in the *Heosemys* stem lineage, and at least once within *Cuora*. A polytomy at the base of *Cuora* (e.g., Spinks et al., 2004; Parham et al., 2004) and a poor understanding of the morphological variation in extent of the temporal arch (see Joyce and Bell 2004) preclude a definitive assessment of the polarity of this character within *Cuora*.

From a biogeographic perspective, the *S. crassicollis* + *H. leytensis* clade seems plausible. *Heosemys leytensis* is known only from the Palawan Pleistocene Aggregate Island Complex (or Palawan PAIC; Brown and Diesmos 2001). Although the Palawan region contains a significant level of endemicity in fauna and flora not found in the Sundaic region (see Widmann 1998, McGuire and Alcala 2000, Brown and Guttman 2002, Evans et al. 2004), in general the fauna of the Palawan PAIC has a much closer affinity to the Islands of the Sunda Shelf (e.g., Kalimantan/'Borneo', Madura, Sumatra) than do the other Philippine islands (Heaney 1986; Brown and Diesmos 2001).

Therefore, the close relationship of *H. leytensis* to a Sunda Shelf species (*S. crassicollis*) is not surprising. The combined distribution of the *S. crassicollis*+*H. leytensis* clade (Fig. 1A) is very similar to that of *Cyclemys dentata* (Gray 1831) and *Cuora amboinensis* (Daudin 1802), the two other turtle species known from Palawan PAIC (Iverson 1992). Their shared distributions may indicate that these three lineages may have a shared biogeographical history as well, the details of which could be compared through additional DNA sequencing of *S. crassicollis*, *Cu. amboinensis* and *Cy. dentata* from throughout their range.

Given the strong phylogenetic signal placing it as the sister taxon to *S. crassicollis*, we feel justified in referring *H. leytensis* to a phylogenetically defined *Siebenrockiella* Lindholm 1929. By using the genus name *Siebenrockiella* to highlight this close relationship, we eliminate two monotypic genera (*Siebenrockiella* and a hypothetical new genus for *H. leytensis*) from a literature that is lamentably crowded with monotypic genera (Spinks et al. 2004). Polytypic genera are functionally superior to monotypic genera because they maximize the information content in each widely-used name (Parham and Feldman 2002; Feldman and Parham 2004). With this is mind, we phylogenetically define *Siebenrockiella* as the crown clade arising from the last common ancestor of *Siebenrockiella* [orig. *Emys*] *crassicollis* (Gray 1831) and *Siebenrockiella* [orig. *Heosemys*] *leytensis* (Taylor 1920) (comb. nov.).

In addition to developing a conservative nomenclature for the widely-used genus name, we also want to name the stem-lineage that includes the morphologically and molecularly divergent *S. leytensis*. For example, compared to *S. crassicollis*, *S. leytensis* has a proportionately larger head and correspondent nuchal emargination, is larger in overall body size, and has an extremely protruding gular region of the plastron (Diesmos et al. 2004b). The morphological distinctiveness of the two known *Siebenrockiella* species is demonstrated by the fact that no author has ever suggested a close relationship between them until now. Moreover, the genetic distinctiveness of the *S. leytensis* lineage is shown by a high sequence divergence from *S. crassicollis* (~13% cyt*b*) that is greater than that shown by other batagurid congeners (5.0-10.7%, see Spinks et al. 2004). In order

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FIGURE 2 (left). Parsimony phylogram of one of the four most parsimonious trees (4387 steps) recovered by the parsimony analysis of the combined cytb and R35 data set for batagurid turtles. For taxonomy of suprageneric clades see Joyce et al. (2004). The four equally parsimonious results differ in the placement of species within the genus *Mauremys* or between suprageneric genera not related to *Heosemys* or *Siebenrockiella*. Nodes that are not supported in all of the four equally parsimonious trees are indicated by '-' on either side of the stem. The numbers at each of the other nodes represent support values. The top numbers are decay indices and the bottom numbers are parsimony bootstrap percentages. Support values for species clades within genera are not shown but see Spinks et al. (2004). The batagurid lineages that lose a complete temporal arch are shown by '*'.

to provide a name for this distinct lineage that is divorced from the vagaries of species concepts, we name a new subgenus, *Panyaenemys*, for *S. leytensis*.

SYSTEMATICS

***Panyaenemys*, new clade name, new subgenus**

TYPE SPECIES: *Siebenrockiella leytensis* (Taylor, 1920) comb. nov.

We designate a type species for this phylogenetically defined clade name so that it is valid under the rules of the International Code of Zoological Nomenclature (1999).

ETYMOLOGY.— *Panyaen-*, from the word 'panya-en' which means 'enchanted' in the language of the Pala'wan (one of seven ethnic groups that inhabit the Palawan islands). A resident of Palawan interviewed by ACD during forest surveys in November, 2003 referred to a *S. leytensis* as a 'panya-en', because it is apparently a favorite pet of forest spirits; *-emys*, turtle.

PHYLOGENETIC DEFINITION.— We define *Panyaenemys* as the most inclusive clade containing *Siebenrockiella* [orig. *Heosemys*] *leytensis* (Taylor 1920) but not *Siebenrockiella* [orig. *Emys*] *crassicollis* (Gray 1831).

DIFFERENTIAL DIAGNOSIS.— The sole known member of the subgenus *Panyaenemys* can be distinguished from all other turtles by the combination of the following four characters: 1) Strongly projecting epiplastra; 2) 'Ginkgo leaf'-shaped vertebral scales 2-4; 3) No temporal arch in the skull; 4) Light lines on the back of the head.

MATERIAL EXAMINED

HEOSEMYS LEYTENSIS.— PHILIPPINES: CAS 60930, the neotype specimen discussed in detail by Buskirk (1989) and Diesmos et al. (2004a); PHILIPPINES: PNM 8488, GenBank accession numbers = AY954911 (cyt*b*) and AY954914 (R35), a dead specimen that was donated to the National Museum of the Philippines (PNM) by a wildlife collector in 2003 and examined by Diesmos et al. (2004b). The specimen was apparently bought from a wildlife trader from Palawan. An additional 47 live specimens of *H. leytensis* in captivity were examined by Diesmos et al. (2004b) comprised of 34 turtles on Palawan being held by a private collector and 13 government-confiscated turtles housed at the Widlife Rescue Center of the Protected Areas and Wildlife Bureau, Quezon City, Philippines.

SIEBENROCKIELLA CRASSICOLLIS.— CAMBODIA: FMNH 259055 (see Stuart and Platt 2004), GenBank accession numbers = AY954912 (cyt*b*) and AY954913 (R35), Koh Kong Province, Sre Ambel District, Prek Kroch River (tributary of Sre Ambel River), 11°06′20″N 103°39′35″E, <10 m elevation, in a flooded paddy at edge of mangrove and *Melaleuca* forest, captured by a fisherman in bamboo fish trap set at that location, 27 August 2000, B.L. Stuart and S.G. Platt; UNCERTAIN/ MALAYSIA?: FMNH 224070, Perak, Batu Gajah, purchased in a pet shop, 19 November 1975, E.O. Moll.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A New Species of *Rhacophorus* (Anura: Rhacophoridae) from Myanmar (Burma)

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A new species of the genus *Rhacophorus* is described from Myanmar. The new species is most similar to *R. bipunctatus* but differs in the male having a larger body size, a bright green dorsal coloration, yellow in the outer portion of the iris, fainter crossbands on the limbs, a more extensive dermal fringe along the arm, more extensive projection on the heel, more extensive webbing on the hand, and typically two large equal-sized black spots, one in the axillary region and one on the middle of the flank.

Ten species of *Rhacophorus* are thought to occur in Myanmar (*R. appendiculatus* (Günther), *R. bipunctatus* Ahl, *R. bisacculus* Taylor, *R. dennysi* Blanford, *R. feae* Boulenger, *R. maximus* Günther, *R. reinwardtii* (Schlegel), *R. taronensis* Smith, *R. turpes* Smith, and *R. verrucosus* Boulenger). Here, we report on an additional species of *Rhacophorus* collected during expeditions in 2001 and 2002 to Rakhine State in western Myanmar near the Bay of Bengal and to Kachin State in northeastern Myanmar near the Chinese border (Fig. 4).

METHODS AND MATERIALS

Specimens were collected by hand, euthanized, tissue samples removed, then fixed in 10% buffered formalin before preserving in 70% ethanol. Latitude and longitude were recorded with a Garmin 12 GPS, datum WGS84. Specimens are housed in the Department of Herpetology, California Academy of Sciences (CAS) and the Division of Amphibians and Reptiles, National Museum of Natural History, Smithsonian Institution (USNM).

The preserved specimens were examined, measured, and compared with available specimens (see material examined; museum acronyms follow Leviton et al. [1985]) and published descriptions of currently recognized (Frost 2004) species of *Rhacophorus* and *Polypedates* from Myanmar and neighboring countries (Boulenger 1920; Smith 1924; Smith 1940; Bourret 1942; Liu and Hu 1961; Taylor 1962; Inger 1966; Berry 1975; Dring 1983; Inger et al. 1985; Sarkar and Sanyal 1985; Inger and Dutta 1986; Kiew 1987; Daniel and Sekar 1989; Yang et al. 1991; Brown and Alcala 1994; Manthey and Grossman 1997; Inger and Stuebing 1997; Iskandar 1998; Chan-ard et al. 1999; Fei 1999; Inger et al. 1999; Das 2000; Ohler et al. 2000; Vasudevan and Dutta 2000; Orlov et al. 2001; Ziegler and Köhler 2001; Chanda 2002; Harvey et al. 2002; Malkmus et al. 2002). Measurements were taken using dial calipers to the nearest 0.1 mm as follows: snout-vent length (SVL, from tip of snout to vent); head length (HL, from tip of snout to hind border of angle of jaw);

head width (HW, width of head at its widest point); internarial distance (IND, distance between nares); interorbital distance (IOD, minimum distance between upper eyelids); snout length (SL, from anterior border of eye to tip of snout); distance from nostril to eye (DNE, from nostril to anterior border of eye); forelimb length (FLL, from elbow to tip of third finger); hand length (HAL, from base of outer palmer tubercle to tip of third finger); thigh length (THL, from vent to knee); tibia length (TIL, from knee to foot); foot length (FL, from proximal end of metatarsal tubercle to tip of fourth toe); width of disk of third finger (3FDW, greatest horizontal width); and width of disk of fourth toe (4TDW, greatest horizontal width).

SPECIES DESCRIPTION

***Rhacophorus htunwini* Wilkinson, Thin Thin, Kyi Soe Lwin, and Awan Khwi Shein, sp. nov.**

Figs. 1-3. Htun Win's treefrog

DIAGNOSIS.— *Rhacophorus htunwini* can be distinguished from all other species of *Rhacophorus* and *Polypedates* by the following combination of characters: intermediate body size in the male (SVL 37.8-50.4 mm); extensive yellow webbing between fingers; thick dermal fringe on forearm and foot, dermal projection (calcar) on heel; squared-off supracloacal fold, snout pointed; bright green dorsal color (slate blue in alcohol); yellow in the outer portion of the iris; very faint crossbands on the limbs; reddish-orange foot webbing; two large black spots on each side of body, one in the axillary region and one at the middle of the flank.

HOLOTYPE.— CAS 229893 (Fig. 1), an adult male, collected from Nagmung Township, Au Yin Ga Camp (27°17′36.9″N, 97°51′45.3″E), Putao District, Kachin State, Myanmar, elevation approximately 878 m, collected on 2 May 2002 by Htun Win, Young Ngai Thi Na, Ram Sar, and Hpe Ram.

DESCRIPTION OF HOLOTYPE.— An adult male with slender habitus and head slightly longer than wide, 36% of SVL; snout pointed in dorsal view, gently slopes in lateral view to nostrils, then becomes slightly spatulate extending beyond mandible (Figs. 1a, c); nostrils closer to eye than tip of snout and anteriorly protuberant; canthus distinct, rounded, and inwardly curved; medial rostral areas between eyes and nostrils and between nostrils and tip of snout slightly concave; lores concave to nostril; eye directed anterolaterally with horizontal pupil. Tympanum distinct and circular; weak supratympanic fold, curving ventrally from dorso-posterior edge of tympanum to posterior edge of axilla.

Vomerine processes with 8/6 rounded teeth respectively and approximately equal to transverse plane, separated medially by a space equal to two times their width, and laterally in contact with anteromedial edge of choanae; choanae small, ovoid to a medial point, and wholly visible at edge of lingual shelves of maxillae when viewed ventrally; tongue deeply bifurcates posteriorly; paired vocal slits oval and lateral to tongue.

Dorsal body surface smooth; ventral abdominal surface and region below thighs areolate; pectoral and gular regions much less areolate. Vent protrudes posteriorly, squared supracloacal fold medially notched.

Arms short and slender; hand 73% as long as foot; when adpressed, relative length of fingers is 3 > 4 > 2 > 1; tips of fingers rounded; digital pads on hands and feet well developed and oval, with circummarginal grooves; distal phalanges bifurcate (as seen from dorsal aspect of digital tips). Hands extensively webbed, webbing formula for digits is **I**2-2**II**1-1**III**1-1**IV** following Myers and Duellman (1982); narrow dermal fringe extends along lateral margin of fourth finger to base of hand. Subarticular tubercles between penultimate and adjoining proximal phalange round and well developed; proximal subarticular tubercles on finger 3 smallest; right hand with one, three, and two

FIGURE 1. (A) Dorsal and (B) ventral views of the body, (C) lateral view of the head, and ventral views of the (D) left hand and (E) left foot of the holotype of *Rhacophorus htunwini* sp. nov. (CAS 229893).

small supernumerary tubercles in a row between proximal tubercle and base of hand on fingers two, three, and four, respectively; left hand with less obvious supernumerary tubercles; thenar tubercle low, extends medially at base of first finger, palmar tubercle absent. Thick dermal flange extends from lateral base of fourth finger to elbow, at widest approximately 18% of width of forearm.

Hind limbs moderately long and slender; when adpressed to body, tibiotarsal articulation reaches beyond anterior edge of eye; webbing on foot reaches to base of pads on all toes; when adpressed, relative length of toes is 4 > 5 = 3 > 2 > 1; thick dermal fringe from base of pad of toe 5 extends along lateral edge of tarsus to heel where it develops into broad flange with laterally projecting calcar on lateral edge of heel. A single subarticular tubercle on toes 1 and 2, two subarticular tubercles on toes 3, 4, and 5; proximal tubercle on toe 5 approximately same size as distal tubercle; supernumerary tubercles and an outer metatarsal tubercle absent; inner metatarsal tubercle flat, oval, and pointed medially.

Coloration in preservative (Fig. 1). Dorsal color of body slate blue, extending laterally and ventrally ⅓ of flanks and limbs, from elbow to halfway up middorsal aspect of hindarm, and along dorsal aspect of forearm, lateral fringe, and lateral half of fourth finger to base of pad, and from vent to knee along middorsal aspect of thigh, entire dorsal aspect of tibia, and lateral half of foot, lateral fringe, and fifth toe to just short of base of pad. Lateral margins of tarsal and supracloacal fringes light cream; first to third fingers and webbing, medial side of forearm, and all but middorsal distal half of hindarm cream yellow; similarly, all but middorsal aspect of thigh, lateral and medial sides of tibia, medial half of foot, and first through fourth toes cream yellow. Webbing between toes two through five with streaks of orange, giving an orange appearance, but cream yellow between toes one and two; small, elongated patch of slate blue on lateral side of second phalange of fourth toe and within webbing at same position between fourth and fifth toes; venter and flanks cream yellow. Posterolateral fringe of lower jaw and midventral aspect of fifth toe with some slate blue pigmentation; cream yellow margin on upper lip. Two large black oval spots on sides in axillary and mid-flank; axillary spot smaller, 8.7 mm horizontal diameter, mid-flank spot larger, 10.8 mm horizontal diameter.

Color in life based on a color transparency (Fig. 2a). Dorsum bright green with sparsely scattered black and white pin-sized spots. Dorsal surface of fingers one through three, toes one through four, all digital pads, webbing on hand, lateral margin of fringe from foot to heel, ventrum, and sides yellow to yellowish orange. Two large jet black spots, with clusters of light blue spots on the dorsal margins, on axillary and mid-flank. Faint crossbands present on dorsal aspect of thigh and tibia.

Pupil surrounded by light grayish brown horizontally rectangular iris, with yellow above and below, more so above. Yellow color extends posterior onto interior of orbit. Black thin line surrounds eye at margin with eyelid.

Variation.— The holotype, paratypes, and referred specimens of *R. htunwini* are male, sexual dimorphism could not be determined. The paratypes and referred specimens are similar to the holotype except for the following. CAS 222065 and 222136 have smaller calcars than holotype. CAS 222065 is much smaller (SVL 37.8 mm), and specimen CAS 222136 has one large black spot in axillary region, without posterior spot on flank. Supratympanic fold of CAS 221351 strong on both sides of head and covers dorsoposterior edge of tympanum, but does so only on left side of CAS 222065, in all other specimens supratympanic fold similar to holotype. The dorsum of CAS 221351 is lighter in coloration than other specimens in alcohol, although color pattern is same, however darker bluish green in life. CAS 221351 has scattered black pin-size spotting on head, dorsum, and dorsal aspect of thighs. Snout of this specimen rounded instead of pointed as in all other specimens, and tips of pads more squared off than other specimens.

Etymology.— The name *htunwini* is given in honor of the late U Htun Win, who devoted the last eight years of his life to the pursuit of knowledge of the diversity and natural history of the reptiles and amphibians within his country. As team leader of the Myanmar Herpetological Survey Team, he first recognized this frog as potentially new to science.

Comparisons.— Because *R. htunwini* is a medium size tree frog that possesses expanded discs on the fingers and toes, an intercalary element between the penultimate and terminal phalanges, a narrow bony metasternum, a flange on the distal end of the third metacarpal, Y-shaped terminal phalanges, and extensive webbing between the fingers and toes, it has been placed within *Rhacophorus* (Wilkinson and Drewes 2000). *Rhacophorus* is a relatively large genus of approximately 60 species from Asia (Frost 2004), and members of this genus closely resemble the approximately 28 species of the genus *Polypedates* (Liem 1970). Because of this close resemblance, several species have been moved back and forth between the two genera, or *Polypedates* has not been

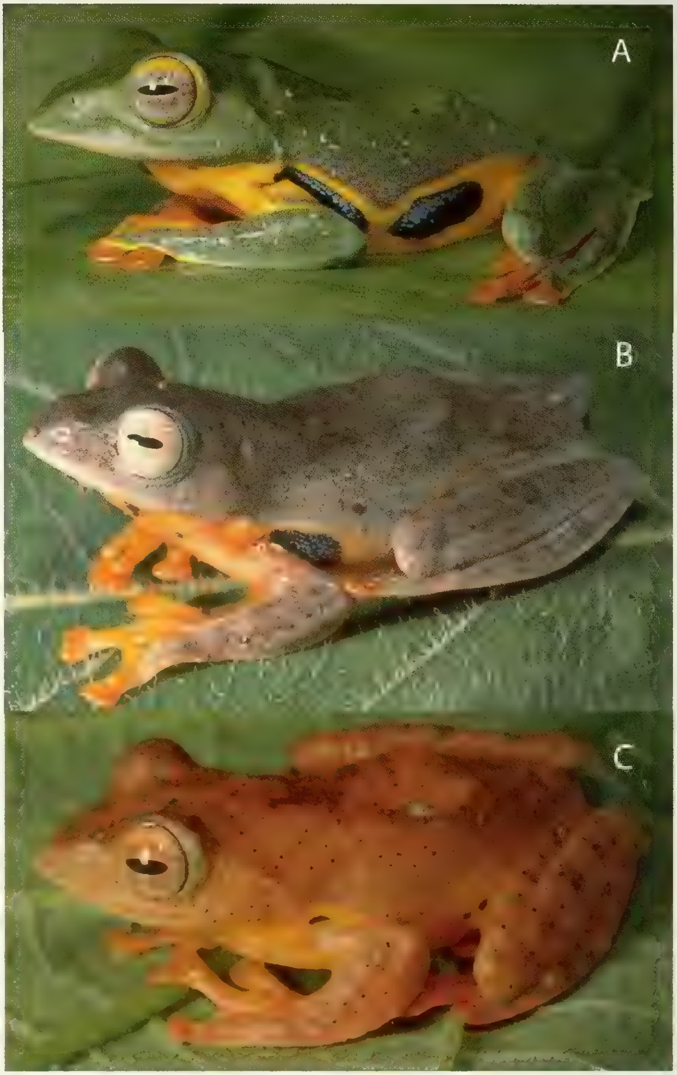

FIGURE 2. Photos in life of (A) a male *Rhacophorus htunwini* sp. nov. (CAS 229893), (B) a female *R. bipunctatus* (CAS 229902), and (C) a male *R. bipunctatus* (CAS 224676).

recognized as a genus separate from *Rhacophorus* (Dubios 1986; Fei 1999). Recently, Wilkinson et al. (2002) provided molecular evidence to separate the genera *Polypedates* and *Rhacophorus*, and to move two species in *Polypedates* (*P. dennysi* and *P. prasinatus*) back into *Rhacophorus*. We believe that generic level reversals are still required in order to ensure the correct taxonomic placement of many species within these two genera and therefore have included members of both genera in the comparisons below.

Following the taxonomic designations in Frost (2004), *R. htunwini* can be distinguished from other species of the following *Rhacophorus* and *Polypedates* from Bangladesh, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Thailand, and Vietnam as follows: from members of *Polypedates* in the *P. leucomystax* species group (*P. colleti*, *P. cruciger*, *P. eques*, *P. leucomystax*, *P. macrotis*, *P. maculatus*, *P. mutus*, *P. otilophus*, and *P. zed*), *P. insularis*, *P. megacephalus*, *P. naso*, *P. pseudocruciger*, members of *Rhacophorus* in the subgenus *Rhacophorus* in the *R. appendiculatus* species group (*R. appendiculatus*, *R. bisacculus*, *R. verrucopus*), *R. baliogaster*, *R. baluensis*, *R. barisani*, *R. bimaculatus*, *R. calcaneus*, *R. catamitus*, *R. cyanopunctatus*, *R. exechopygus*, *R. margaritifer*, *R. modestus*, *R. namdaphaensis*, *R. orlovi*, *R. poecilonotus*, *R. translineatus*, *R. tuberculatus*, and *R. verrucosus* by a bright green dorsal color; from members of *Polypedates* in the *P. chenfui* species group (*P. chenfui*, *P. hungfuensis*, and *P. yaoshanensis*), the *P. dugritei* species group (*P. dugritei*, and *P. omeimontis*), *P. dorsoviridis*, *P. duboisi*, *P. nigropunctatus*, *P. pingbianensis*, *P. puerensis*, *P. zhaojuensis*, members of *Rhacophours* in the subgenus *Rhacophorus* and the *R. dennysii* species group (*R. dennysi* and *R. feae*), the *R. pardalis* species group (*R. annamensis*, *R. notator*, *R. pardalis*, and *R. robinsonii*), *R. achantharrhena*, *R. angulirostris*, *R. taronensis*, and *R. variabilis* by the presence of a sharp dermal calcar at the heel; from members of *Rhacophorus* in the subgenus *Rhacophorus* and

FIGURE 3. Dorsal view of representative specimens of *Rhacophorus htunwini* sp. nov. (top row), representative specimens of female *R. bipunctatus* (middle row), and representative specimens of male *R. bipunctatus* (bottom row).

the *R. malabaricus* species group (*R. calcadensis* and *R. malabaricus*), *R. lateralis*, *R. pseudomalabaricus,* and *R. turpes* by axillary spots.

Rhacophorus htunwini closely resembles members of the *R. reinwardtii* species group in the subgenus *Rhacophorus* (*R. bipunctatus*, *R. dulitensis*, *R. maximus*, *R. nigropalmatus*, *R. prominanus*, *R. reinwardtii*) and *R. hoangliensis*, but can be distinguished from all but *R. bipunctatus* and *R. reinwardtii* by the presence of axillary spots. It can be distinguished from *R. reinwardtii* (SVL male 68 mm) by its smaller size and yellow hand webbing (black hand webbing in *R. reinwardtii*).

Rhacophorus htunwini most closely resembles *R. bipunctatus*, which also has axillary spots, dermal calcars at the heels, a pointed snout, and sometimes a green dorsal color (Fig. 2b). However, it can be distinguished from *R. bipunctatus* by size (Table 1, Fig. 3); the males of *R. htunwini* are larger (average SVL = 45.7 mm) than the males of *R. bipunctatus* (average SVL = 34.9 mm). *Rhacophorus htunwini* also has a bright green dorsal color in life that becomes slate blue when preserved, whereas some members of *R. bipunctatus* have an olive green dorsal color in life that becomes light bluish gray or brown when preserved and others are orange to tan in life with a darker brown pattern (blotching or an X mark) on the dorsum, which become brown when preserved (Figs. 2–3). The eye of *R. htunwini* contains yellow at the upper and lower portion of the iris, which is absent in *R. bipunctatus* (Fig. 2). *Rhacophorus bipunctatus* has distinct crossbands on the fore and hindlimbs (Figs. 2b–c), whereas *R. htunwini* has faint crossbands that disappear in alcohol (Fig. 2a). *Rhacophorus htunwini* has a more extensive dermal fringe on the forearm, a more extensive dermal calcar at the heel, and more extensive webbing on the hand than the male of *R. bipunctatus*. In all but one specimen, *R. htunwini* has two large black equal size spots on the sides, one in the axillary region and one on the flank, whereas, the majority of male specimens of *R. bipunctatus* examined had only one spot in the axillary region, and in specimens that had two spots the posterior spot was much smaller than the anterior spot.

Distribution and Natural History.— At present *Rhacophorus htunwini* is known from Nagmung and Machanbaw Townships, Putao District, Kachin State, and from much further south in Rahkine State in the southwestern foothills of Rakhine Yoma, Gwa Township, and Kyauktaw Township, Sittawe District (Fig. 4). This distributional pattern indicates that this species may be restricted to the Indo-Burman Mountain Range that arcs from southwestern Myanmar along the border with India, and the Eastern Himalayas in northern Myanmar. The absence of specimens from the Chin Hills of western Myanmar is probably due solely to a lack of surveys in the region.

The type specimens including the holotype (CAS 229913, USNM 561869) were found approximately 2 m off the ground in bamboo. Referred specimens were found in undisturbed habitat near a spring (CAS 222136) or seasonal (CAS 221351) and permanent (CAS 222065) streams. Other species of *Polypedates* and *Rhacophorus* found in the vicinity of the type locality were *P. leucomystax*, *R. bipunctatus*, and *R. dennysi*.

Figure 4. Distribution of *Rhacophorus htunwini* sp. nov. in Myanmar with type locality indicated by a star (at tip of arrow).

Material Examined

Rhacophorus htunwini (paratypes): CAS 229913, USNM 561869 adult males collected at the same locality and date as the holotype.

Rhacophorus htunwini (referred specimens): CAS 221351, an adult male, collected between Ahtan Ga and Au Rin Ga (27°15′27.2″N, 97°50′32.4″E), Ma Chan Baw Township, Putao District, Kachin State, Myanmar, collected on 4 September 2001 by Htun Win and Ran Shaung; CAS 222136, an adult male, collected from Yea Pu Camp (17°56′02.6″N, 94°38′02.9″E), Gwa Township, Rakhine State, Myanmar, collected on 8 June 2001 by Hla Tun, Kyi Soe Lwin, and Awan Khwi Shein; CAS 222065, an adult male, collected from Pin Lone Camp, Pe Chaung, near Saba Sate Village (21°00′54.9″N, 92°52′06.6″E), Kyaut Taw Township, Sittawe District, Rakhine State, Myanmar, collected on 4 July 2001 by Htun Win, Kyi Soe Lwin, and Awan Khwi Shein.

Polypedates chenfui: FMNH 232963, 232964 (China).

Polypedates colletti: FMNH 234773, 235631 (Malaysia).

Polypedates cruciger: CAS 85280 (Sri Lanka).

Polypedates dugritei: CAS 64273 (China).

Polypedates eques: CAS 85281, 85282 (Sri Lanka).

Polypedates leucomystax: FMNH 239159 (Malaysia); FMNH 254649 (Lao PDR); CAS-SU 15163 (India); CAS 14943 (China); CAS 94573 (Bangladesh); CAS 103624 (Indonesia); CAS 105003 (Vietnam); CAS 105972 (Malaysia); CAS 111336 (Cambodia); CAS 172691 (Thailand); CAS 221962, 224461 (Myanmar).

Polypedates macrotis: FMNH 239107, 239119 (Malaysia); CAS 60630, 60631, 60684, 60804, 62138 (Philippines); CAS 62581 (Malaysia); CAS 64074 (Philippines); CAS 64077 (Indonesia); CAS 64089–64092 (Philippines); CAS 105974, 105975 (Malaysia).

Polypedates maculates: CAS 16922–16924 (Sri Lanka); CAS 94571, 94572, 104152, 125365–125370 (India).

Polypedates megacephalus: ROM (field numbers) 18038, 18045 (Vietnam).

Polypedates otilophus: FMNH 230836, 239147 (Malaysia).

Rhacophorus angulirostris: FMNH 235035 (Malaysia).

Rhacophorus annamensis: FMNH 253933, 253940 (Vietnam); ROM 29889, 29890, 29891, 29892, 29897, 29901, 29904 (Vietnam).

Rhacophorus appendiculatus: CAS 60169–60174, 62261, 64078–64086 (Philippines).

Rhacophorus bimaculatus: CAS 61840, 133178–133180, 133251 (Philippines).

Rhacophorus bipunctatus: FMNH 253122, 253124 (Vietnam); NMNS 3220 (China); CAS 224676, 228808, 229887, 229889, 229890, 229898, 229899, 229901–229907, 229910 (Myanmar).

Rhacophorus calcaneus: FMNH 256456, 257933 (Lao PDR); ROM 29849, 29850, 29854, 29855, 29875, 29877, 29879, 29880 (Vietnam).

Rhacophorus dennysi: FMNH 256449, 256450 (Lao PDR); ROM 29839, 29840, 29841, 29842, 29843, 29846, 30245 (Vietnam); CAS 64224 (China); CAS 221535, 224496, 224659 (Myanmar).

Rhacophorus dulitensis: FMNH 235741 (Malaysia).

Rhacophorus feae: FMNH 257910 (Lao PDR); CAS-SU 6387, 6388 (Vietnam).

Rhacophorus gauni: FMNH 235044, 239238 (Malaysia).

Rhacophorus maximus: CAS 221516, 221517 (Myanmar).

Rhacophorus microtympanum: CAS 85283 (Sri Lanka).

Rhacophorus nigropalmatus: FMNH 230901, 230902 (Malaysia).

Rhacophorus pardalis: FMNH 235750 (Malaysia); FMNH 259530 (Philippines); CAS 60472–60476, 61386, 128725, 129267–126270 (Philippines).

Rhacophorus reinwardtii: FMNH 235034 (Malaysia), FMNH 255305 (Lao PDR); NMNS 3213 (China).

Rhacophorus rufipes: FMNH 231377 (Malaysia).

Rhacophorus taronensis: BMNH 1947.2.8.17 (Myanmar).

Rhacophorus turpes: BMNH 1947.2.8.69, 1947.2.8.70 (Myanmar).

Rhacophorus verrucosus: CAS 224441, 224442, 224469, 224737, 224754, (Myanmar).

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Appendix

TABLE 1. Measurements of the type series and referred specimens of *Rhacophorus htunwini* and comparative material of *R. bipunctatus*. Mean (in mm) followed by range (in parenthesis) and ratio of SVL (below). See text for abbreviations.

	Rhacophorus htunwini	*Rhacophorus bipunctatus*	*Rhacophorus bipunctatus*
	Male	Female	Male
	N = 6	N = 3	N = 16
SVL	45.7 (37.8-50.4)	55.9 (51.2-60.2)	34.9 (32.0-37.7)
HL	16.4 (13.5-17.7)	18.3 (17.2-19.8)	12.5 (11.5-14.0)
	35.9	32.7	35.9
HW	16.5 (14.9-17.5)	17.9 (16.9-19.3)	12.6 (11.4-14.1)
	36	32.1	36
IND	4.4 (4.3-4.9)	4.5 (4.4-4.7)	3.4 (2.7-4.2)
	9.6	8.1	9.8
IOD	5.2 (4.8-5.9)	6.6 (5.4-7.5)	3.8 (2.9-4.5)
	11.4	11.8	10.9
SN	7.3 (6.1-8.1)	8.0 (7.7-8.4)	5.4 (4.6-6.0)
	16	14.2	15.6
DNE	3.7 (3.1-4.2)	3.6 (3.2-4.0)	2.6 (2.1-2.9)
	8	6.4	7.4
FLL	22.0 (18.6-25.1)	27.9 (26.8-29.2)	17.9 (16.1-19.7)
	48.1	49.8	51.2
HL	13.8 (11.2-15.5)	17.6 (16.5-19.0)	11.2 (10.0-12.5)
	30.3	31.4	32
THL	22.5 (17.6-26.1)	27.0 (26.7-27.4)	17.6 (14.3-19.7)
	49.3	48.2	50.5
TIL	23.0 (19.4-25.1)	26.2 (25.0-27.9)	17.5 (15.6-18.7)
	50.3	46.9	50.3
FL	20.0 (16.2-22.3)	25.9 (24.8-27.9)	15.6 (13.9-16.9)
	43.7	46.3	44.7
3FDW	2.5 (2.2-2.7)	3.2 (3.1-3.4)	1.9 (1.5-2.4)
	5.4	5.8	5.4
4TDW	1.9 (1.6-2.2)	2.4 (2.0-2.7)	1.5 (1.2-1.9)
	4.2	4.3	4.2

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New Taxa of Octocorals (Anthozoa: Octocorallia) from the Northeastern Pacific Ocean

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The octocorallian fauna of the Alaskan region is poorly known. Recently, several research projects have been initiated to explore the faunal elements of the continental shelf in the Gulf of Alaska. A wealth of material, including octocorals (mostly gorgonians with some pennatulaceans), has been collected by trawl nets during field research conducted by agencies such as the National Marine Fisheries Service (NMFS) of the National Oceanic and Atmospheric Administration (NOAA). A new genus of gorgonian has recently been described from the Aleutian Islands as *Alaskagorgia* Sanchez and Cairns, 2004. The present paper reports the discovery of an additional plexaurid gorgonian from the same region, and provides a description of it as a new genus and species. Additionally, an unusual new species of sea pen, genus *Cavernularia* (Family Veretillidae), is described from the central Aleutian island chain. The geographically nearest veretillid taxa outside of the type locality occur in the northwestern and eastern Pacific — Japan and Panama.

According to Wing and Barnard (2004), approximately 64 species of octocorals are presently known to occur in Alaskan waters. The authors also provide a key to the known octocoral taxa and color figures for twenty species. Other kinds of coral also included are scleractinians, stylasterine hydrocorals, and antipatharians.

The gorgonian family Plexauridae Gray, 1859 has relatively recently had a plethora of genera allocated to it along with the amalgamation of several groups at the ranks of family and subfamily. Included here are the Muriceidae, Paramuriceidae, Plexaurinae, and Stenogorgiinae (= Paramuriceinae) (Bayer 1981). The tropical western Atlantic genera were treated by Bayer (1961). Recent works have compiled previously described taxa and have added new generic names making a total of approximately 38 genera that are presently considered to comprise the family. These works include Grasshoff (1977) for the northern Atlantic Ocean and Mediterranean Sea, Grasshoff and Barbigant (2001) and Frabricius and Alderslade (2001) for the tropical western Pacific, and Sanchez and Cairns (2004) for Alaskan waters. The present paper describes an additional new genus and species from the Alaskan Aleutian Islands, making a total of 39 worldwide genera in the family Plexauridae. The new taxon does not closely resemble other plexaurid taxa.

In addition, a new species of the veretillid pennatulacean genus *Cavernularia* is described, also from the Aleutian Archipelago. The only other known taxa of vertetillid pennatulaceans from the northwestern and eastern Pacific Ocean include several species from Japan, Panama, and the Galápagos Islands (López-González, Gili, and Williams 2000; Kükenthal 1915; Hickson 1921; and Williams 1989, 1995).

METHODS

Material was collected on board a research vessel (the F/V "Vesteraalen" or the M/V "Sea Storm") using trawling gear, and was preserved in 75% ethanol. Sclerites were isolated from surrounding tissues by the use of sodium hypochlorite (household bleach). Micrographs were made using a Nikon Coolpix 990 digital camera, sometimes in combination with a Nikon SMZ-10 dissecting microscope or an Olympus CH-2 compound microscope. Original drawings of sclerites were made with an Olympus CH-2 compound microscope and an Olympus drawing tube. Scanning electron micrographs were taken using a LEO 1400 series scanning electron microscope. Digital images for the making of plates were manipulated using Adobe Photoshop software. Abbreviations used in the text are CAS (California Academy of Sciences, San Francisco), NMFS (National Marine Fisheries Service), and NOAA (National Oceanic and Atmospheric Administration — of the United States Department of Commerce).

SYSTEMATIC ACCOUNT

Order Alcyonacea Lamouroux, 1816
Family Plexauridae Gray, 1859

REMARKS.— Most of the taxa allocated to this family have relatively large sclerites, over 0.3 mm long (up to a maximum length of approximately 5 mm), with tubercular sculpture rarely arranged in whorls. In addition, both Bayer (1981:924) and Fabricius and Alderslade (2001:59) use the following axial characteristics to describe the family. The plexaurid axis often appears woody and fibrous, often brown or darker. The central core is wide, hollow, and cross-chambered. The surrounding axial cortex is soft, usually with hollow spaces called loculi that are sometimes filled with a fibrous substance or non-spicular calcite. In contrast, the family Gorgoniidae usually has small scerites, less than 0.3 mm long, with tubercles arranged in whorls. The axis is often dark brown or black. It has a narrow core and the cortex is very dense with few or no locules.

The new taxon described here is somewhat enigmatic in that it has small scerites, less than or equal to 0.15 mm in length, which is characteristic of the Gorgoniidae. Additionally, the tubercles of the spindles and radiates are sometimes arranged in whorls, but often they are not. Regardless of the problematic nature of these features, the new taxon is here placed in the family Plexauridae because the axis has a woody or fibrous appearance and wide and hollow central core, whereas the surrounding axial cortex is soft with easily observable amounts of non-spicular calcite (Fig. 1).

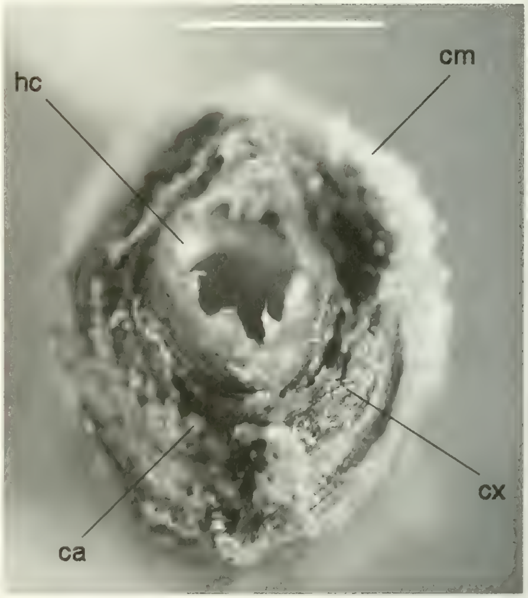


FIGURE 1. Non-type specimen (CAS 164584) of *Cryogorgia koolsae* gen. and sp. nov. Transverse section of a branch near the apical end showing the axis and thin coenenchyme; scale bar = 3.8 mm; **ca** – calcitic material, **cm** – coenenchyme, **cx** – axial cortex, **hc** – hollow core.

Genus *Cryogorgia* Williams, gen. nov.

TYPE SPECIES: *Cryogorgia koolsae* Williams, sp. nov., by monotypy

DIAGNOSIS.— Branching relatively sparse, mostly lateral but rarely dichotomous, planar, anastomosis absent. Terminal branches elongate, somewhat clavate. Azooxanthellate. Axis proteinaceous, flexible with wide hollow core, brown to dark brown, cylindrical near holdfast, slightly compressed in higher branches. Polyps monomorphic, retractile into polyp mounds or completely into coenenchyme, calyces absent. Coenenchymal sclerites leaf clubs, coarsely-tuberculated spindles, radiates, modified and often clavate radiates (some approaching wart clubs), and crosses. Sclerites colorless. Wet-preserved coenenchyme tan-white.

ETYMOLOGY.— The new generic name is derived from the Greek, *Kryos* (cold or chilly) and the commonly used suffix for a gorgonian octocoral, *-gorgia*; in reference to the cold nature of the type locality of this gorgonian.

Cryogorgia koolsae Williams, sp. nov.

Figs. 1–8

MATERIAL EXAMINED.— HOLOTYPE: CAS 151364, Northeastern Pacific Ocean, United States, Alaska, Aleutian Islands, 52.25°N 171.70°W, 406 m depth, Haul 79, 11 June 2000, collected by E.J. Kools aboard F/V "Vesteraalen," NMFS Aleutian Survey 2000, one whole colony wet preserved in 75% ethanol. PARATYPE: CAS 150650, Northeastern Pacific Ocean, United States, Alaska, Aleutian Islands, 52.07° N 177.25° W, 86 m depth, Haul 146, 26 June 2000, collected by E.J. Kools aboard F/V "Vesteraalen," NMFS Aleutian Survery 2000, one whole colony wet preserved in 75% ethanol. OTHER MATERIAL: CAS 164584, Northeastern Pacific Ocean, United States, Alaska, Aleutian Islands, 51.75°N 175.67°W, 83 m depth, Haul 101, 7 July 2002, collected by R.J. Van Syoc aboard M/V "Sea Storm," three whole colonies wet preserved in 95% ethanol. CAS 168893, Northeastern Pacific Ocean, United States, Alaska, Aleutian Islands, 52.31°N 173.65°W, 402 m depth, Haul 144, collected by R.J. Van Syoc aboard M/V "Sea Storm," one whole colony wet preserved in ethanol.

DESCRIPTION OF HOLOTYPE.— Growth form and size (Figs. 2–3): The holotype measures 370 mm long by 150 mm wide. The basal trunk is 115 mm in length before the first side branch arises. It averages approximately 10 wide and 8 mm deep, as it is slightly compressed. The branching is irregular (lateral) and sparse. The terminal branches are 30–100 mm in length.

Polyps (Figs. 3A–E): The polyps of the holotype exhibit various states of retractility. Some are preserved totally retracted and flush with the surrounding coenenchyme — especially those along the main stem and along the thicker branches, whereas others are preserved in various stages of exsertion. The length of the exserted polyps is usually less than 2 mm. They vary in shape from mound-like and hemispherical to cone-shaped or somewhat cylindrical (Fig. 3E). These mounds or cones are thickly set with coenenchymal sclerites (Fig. 5). In all cases, the anthocodiae are at least partly retracted or hidden. Examination of dissected polyps has not shown the anthocodiae to contain sclerites.

Sclerites (Figs. 2C, 4–7): Coenenchymal sclerites of the polyp-bearing branchs, branch tips, and polyp mounds are of several different forms: foliates or leaf clubs (0.07–0.12 mm in length); seven- and eight-radiates (0.07–0.10 mm long); clavate forms (0.08–0.15 mm in length); crosses (0.10–0.11 mm long); and modified radiates, cylinders, and spindles (0.07–0.15 mm in length). Anthocodial sclerites are apparently absent.

Color (Figs. 2–3): The axis is dark brown to black. The coenenchyme and retracted polyps are grayish white to tan-white. The sclerites are colorless.

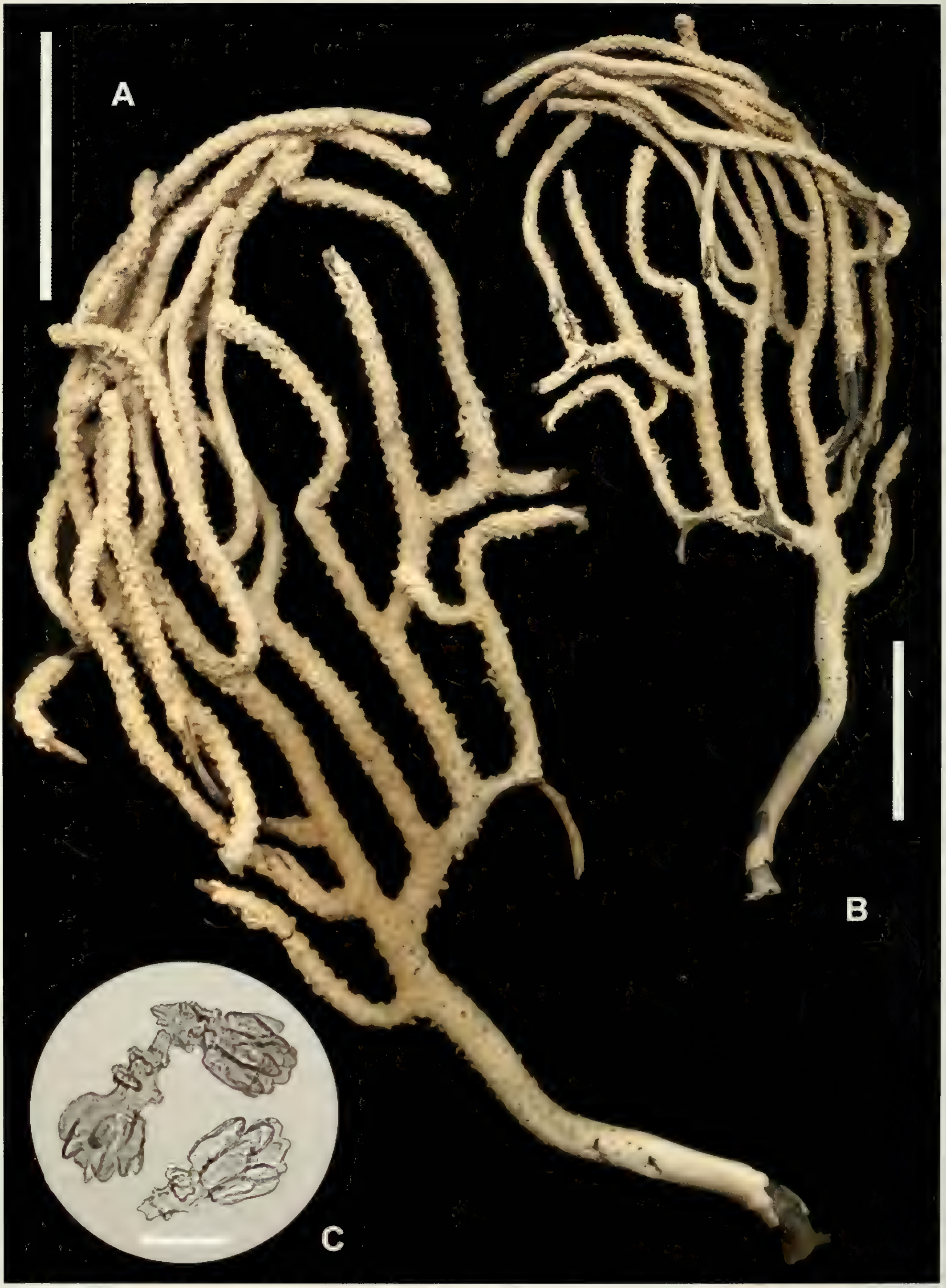


FIGURE 2. A–B. Holotype of *Cryogorgia koolsae* gen. and sp. nov.; scale bars = 65 mm. C. Three leaf club sclerites from the surface coenenchyme of a terminal branch; scale bar = 0.05 mm.

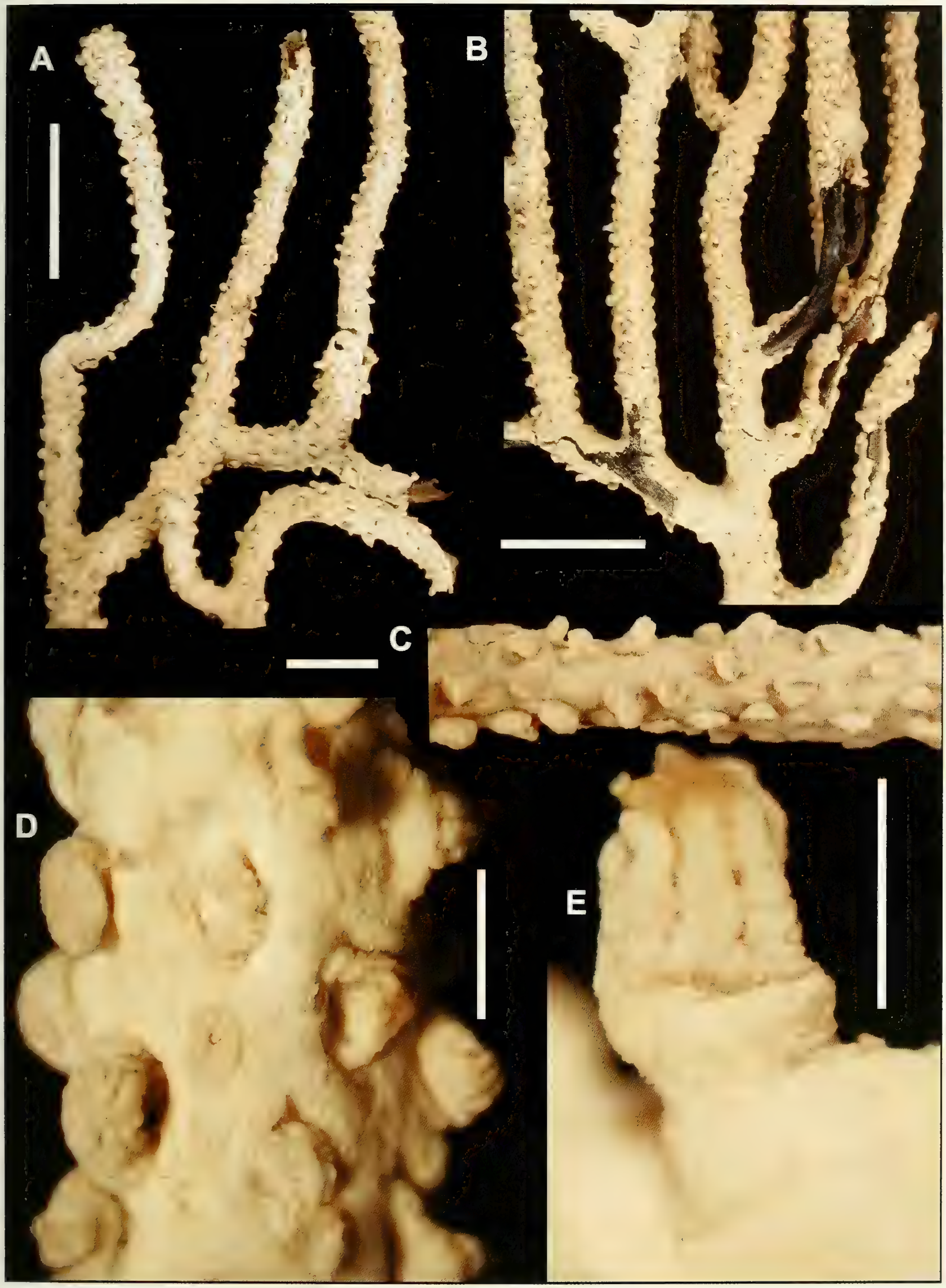


FIGURE 3. Holotype of *Cryogorgia koolsae* gen. and sp. nov.; details of branches and polyps. A–B. Details of branching patterns. C–D. Details of a single branch and polyps. E. Detail of a single polyp. Scale bars: A = 25 mm, B = 25 mm, C = 5 mm, D = 2 mm, E = 1 mm.

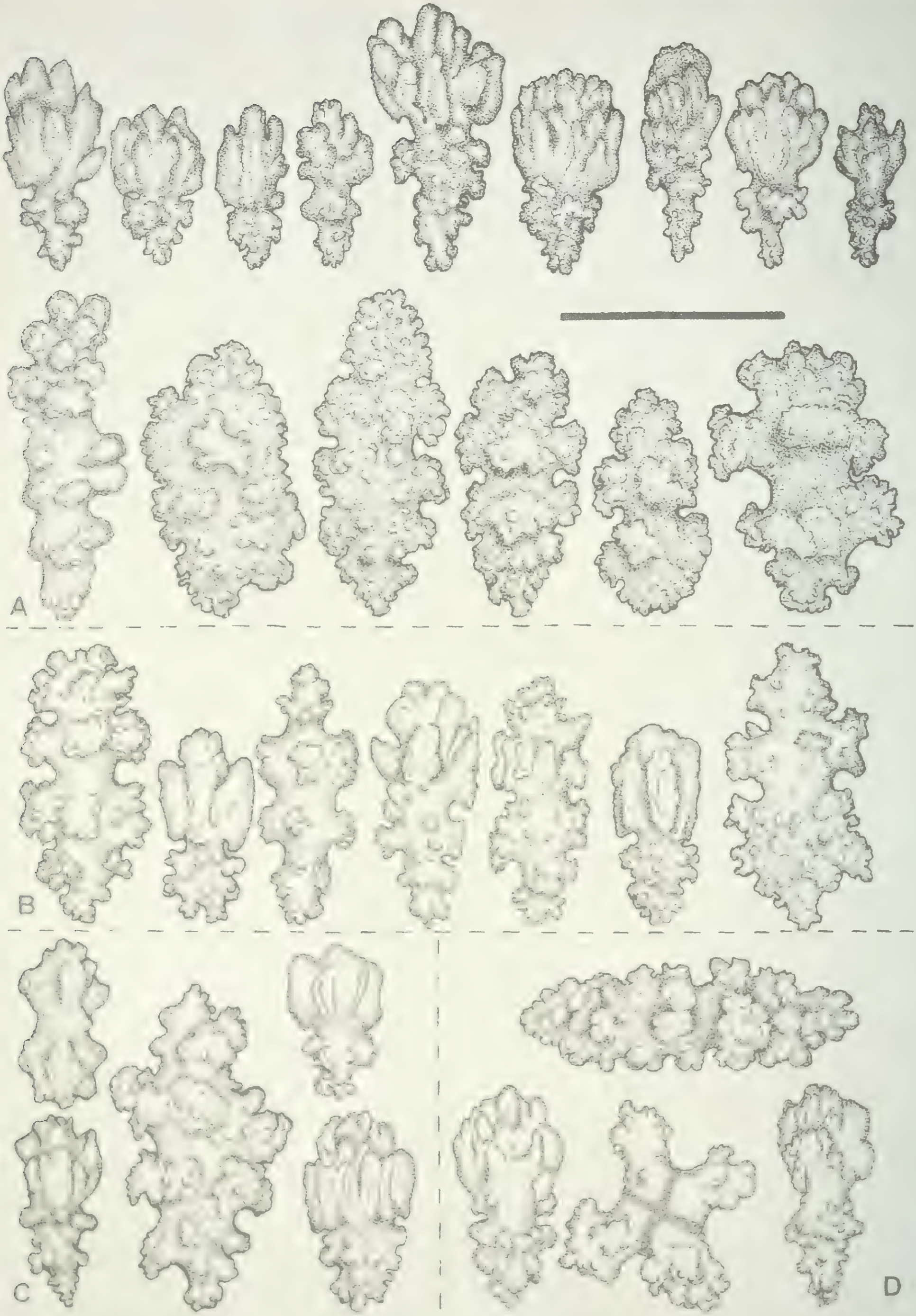
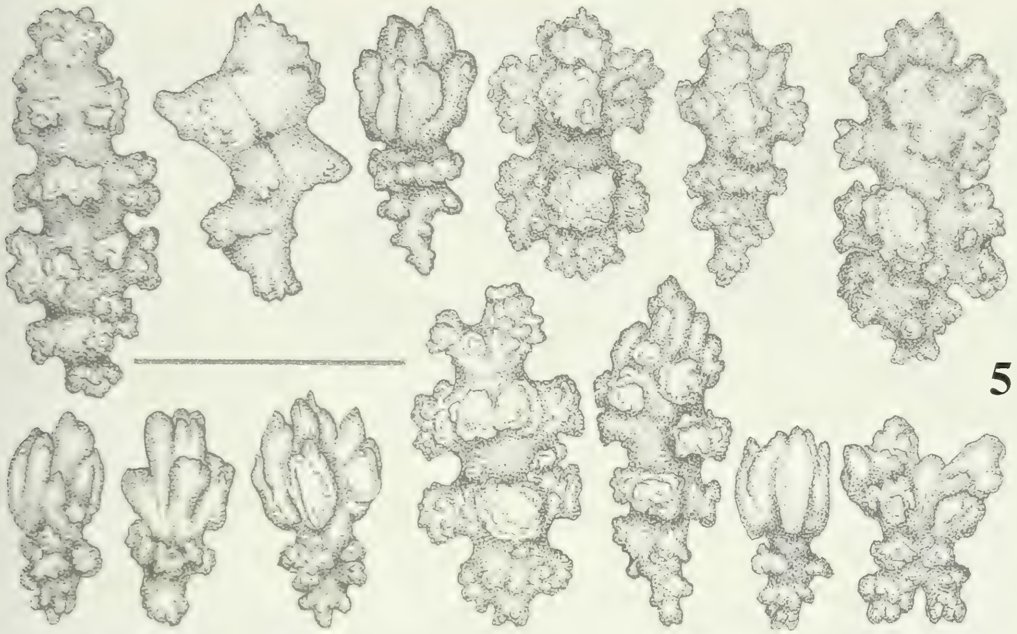


FIGURE 4. *Cryogorgia koolsae* gen. and sp. nov. Coenenchymal sclerites from a polyp-bearing branch; scale bar = 0.10 mm. A. Holotype (CAS 151364). B. Paratype (CAS 150650). C. Non-type specimen (CAS 164584). D. Non-type specimen (CAS 168893). Scale bar = 0.10 mm.



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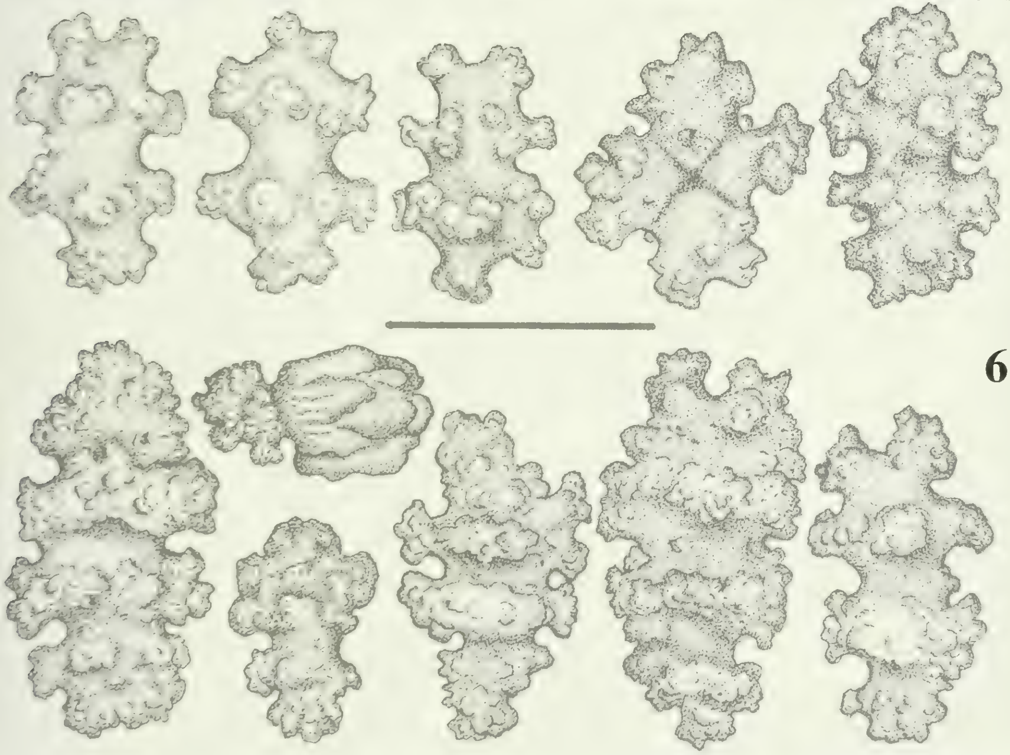

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FIGURE 5 (above) *Cryogorgia koolsae* gen. and sp. nov. Coenenchymal sclerites from a mound formed by a retracted polyp; scale bar = 0.10 mm. FIGURE 6 (below). Holotype of *Cryogorgia koolsae* gen. and sp. nov. Coenenchymal sclerites from the base of the holdfast; scale bar = 0.10 mm.

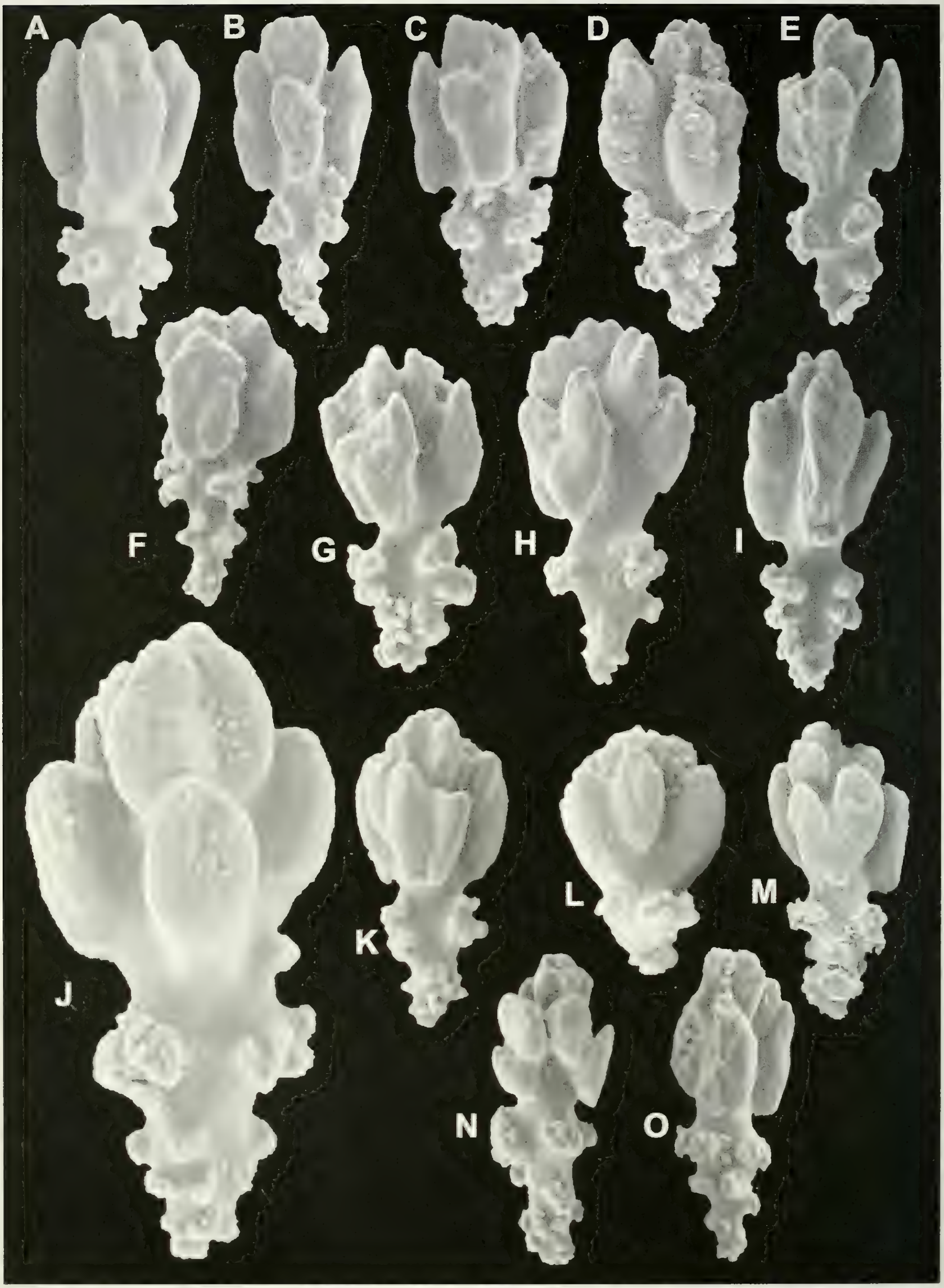

FIGURE 7. Holotype of *Cryogorgia koolsae* gen. and sp. nov. Scanning electron micrographs of leaf clubs from the coenenchyme of a terminal branch. A. 0.08 mm. B. 0.11 mm. C. 0.08 mm. D. 0.08 mm. E. 0.09 mm. F. 0.08 mm. G. 0.07 mm. H. 0.09 mm. I. 0.08 mm. J. 0.10 mm. K. 0.08 mm. L. 0.06 mm. M. 0.10 mm. N. 0.12 mm. O. 0.10 mm.

Etymology.— This species is named for its discoverer, Elizabeth J. Kools, (Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco).

Distribution.— This new taxon is presently known from four localities in the central Aleutian Archipelago of Alaska, northern Pacific; 83–406 m depth (Fig. 8).

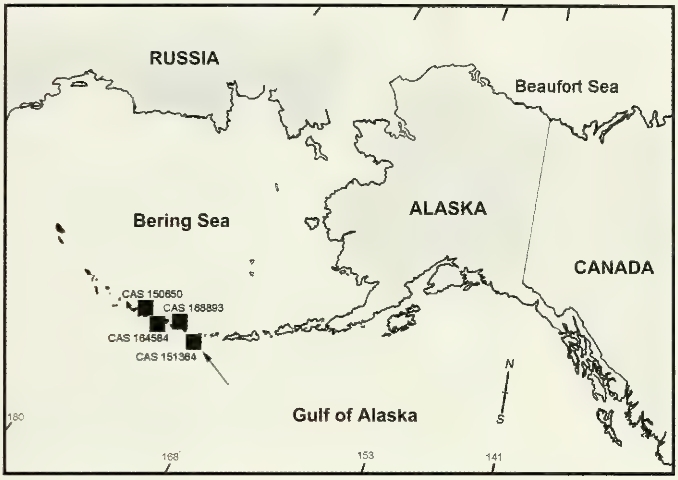

FIGURE 8. Map of the Aleutian Island Chain showing collecting stations (with collection numbers) for *Cryogorglia koolsae* gen. and sp. nov. (■); arrow shows type locality.

Order Pennatulacea Verrill, 1865

Family Veretillidae Herklots, 1858

Genus *Cavernularia* Valenciennes in Milne-Edwards and Haime, 1850

***Cavernularia vansyoci* Williams, sp. nov.**
Figs. 9–10

Material Examined.— Holotype: CAS 168894, Northeastern Pacific Ocean, United States, Alaska, Aleutian Islands, 52.0663° to 52.07043°N; 175.30231° to 175.2824°W, 86–93 m depth, Haul Number 66, 13 June 2002, collected by Robert Van Syoc on board M/V "Sea Storm," NMFS Aleutian Survey 2002, one whole colony cut longitudinally into two halves and wet preserved in 75% ethanol.

Description of holotype.— Growth form and size (Figs. 9A–B, 10A): The colony is clavate, 33 mm in total length.

Polyps (Figs. 9A–D, 10A): The polyps of the holotype are all preserved completely retracted. They are flush with the surface of the rachis and nowhere do they extend past the surface. Calyces are absent. The polyps and polyp walls contain minute sclerites, similar to the sclerites of the surperficial coenenchyme and peduncular interior. As in the coenchymal tissues, these sclerites can only accurately be detected at microscope magnifications at 400× or higher.

Internal Anatomy (Figs. 9C–D): The specimen was cut longitudinally into two halves to reveal internal structures. Gastric cavities are approximately 1 mm wide and 4–5 mm long. Numerous ova can be concentrated in interior-most parts of some of the cavities. In the center of the colony, several vertical canals can be seen. A calcified axis is absent altogether.

Sclerites (Figs. 9E, 10B–C). The sclerite complement is composed entirely of very small ovals

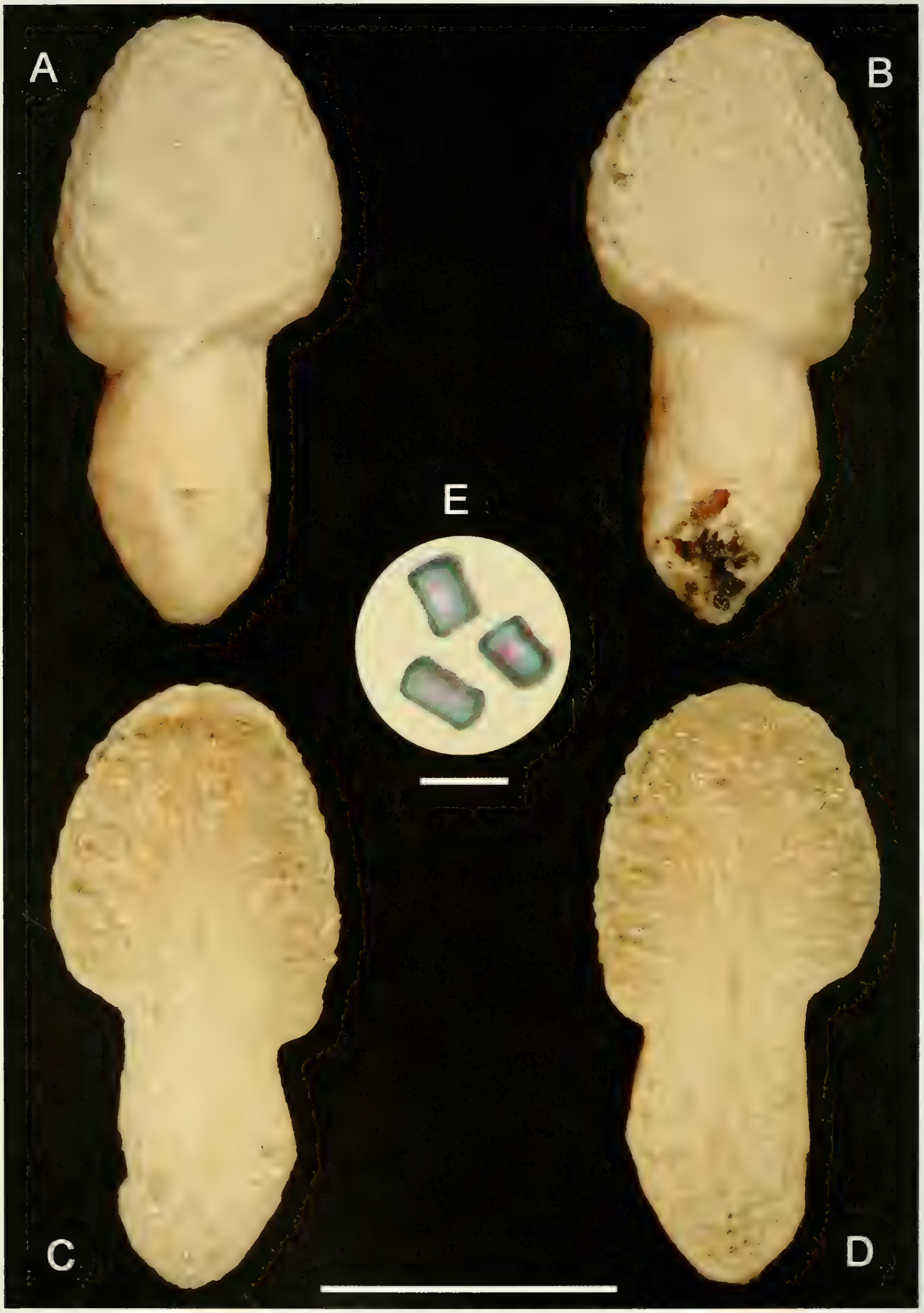

FIGURE 9. *Cavernularia vansyoci* sp. nov. A–B. External views of both halves of the longitudinally sectioned holotype. C–D. Internal views of both halves of the longitudinally sectioned holotype. E. Photomicrographs of three sclerites from the superficial coenenchyme taken from the region of juncture between the rachis and peduncle of the holotype: the sclerites are actually colorless, color shown here is due to properties of the light microscope at high power. Scale bar for A-D = 16 mm; scale bar for E = 0.005 mm.

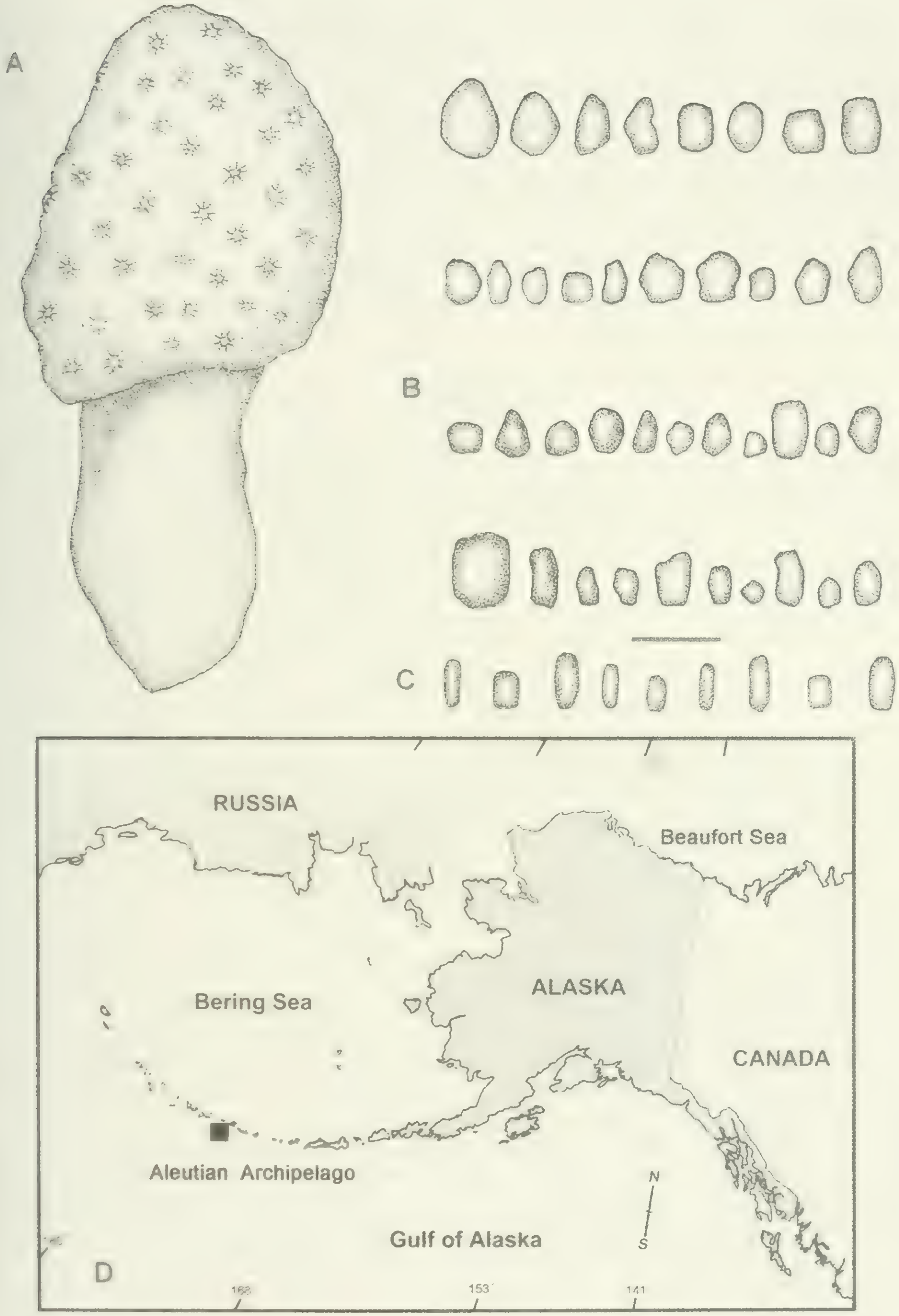

FIGURE 10. *Cavernularia vansyoci*, sp. nov. A. Whole wet-preserved holotype, 33 mm in length. B. Coenenchymal sclerites from the surface of the junction between the rachis and the peduncle. C. Sclerites from the interior of the peduncle. Scale bar for B and C = 0.01 mm. D. Map showing locality of the holotype (■ = collecting station).

(0.003–0.007 mm in length). The shape of these sclerites is only accurately discernable at microscopic magnifications of 400x or more. They vary in shape from rounded-rectilinear to oval, more-or-less round, or elliptical. Some sclerites are irregular in shape. These minute sclerites are relatively dense is all parts of the colony examined, including the coenenchyme of the surface of the rachis and peduncle, as well as the interior of the colony, but seem to be less densely distributed in the anthocodiae and polyp walls.

Color (Figs. 9A–D). The color of the preserved holotype is grayish white throughout. The sclerites are colorless.

Etymology.— This species is named for its discoverer, Robert Van Syoc, Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco.

Distribution.— The new species is known only from the type locality in the Aleutian Islands of Alaska; 86–93 m depth (Fig. 10D).

Discussion

The most recent compendium of Alaskan corals is that of Wing and Barnard (2004), which includes a listing of twelve species of plexaurid octocorals and twelve species of pennatulaceans. Of these, three plexaurids and three pennatulaceans are figured with color photographs. The taxa figured are identified as belonging to five genera — *Muriceides*, *Swiftia*, *Protoptilum*, *Ptilosarcus*, and *Halipteris*. The present paper describes a new genus and species of plexaurid gorgonian and a new species of the pennatulacean genus *Cavernularia* — these are newly recorded taxa to the Alaskan octocoral fauna.

Acknowledgments

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A New Species of *Marionia* (Gastropoda: Nudibranchia) from the Caroline Islands

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A new species of tritoniid nudibranch is described from the western Caroline Islands. *Marionia bathycarolinensis* is known only from its type location of Palau. This animal exceeds 10 cm in length, is reddish in color and is the second record from the Indo-Pacific region of a tritoniid with more than 20 pairs of branchial plumes. Internally, it is distinguished from other Indo-Pacific tritoniids by jaws with masticatory borders composed of multiple rows of rodlets, a broad radula with elongate and distinctively shaped rachidian teeth, and a proportionally long esophagus. A muscular band carries approximately 50 chitinous plates arranged so their distal edges face the lumen of the stomach. Analysis of stomach contents shows that the holotype was feeding on octocorals of the genus *Paracis*. This is the first record of a nudibranch feeding on this genus. Placement of the new species in the genus *Marionia* is discussed in the light of taxonomic problems brought about by the treatment of the group by Odhner (1963).

The current state of knowledge of the tritoniid nudibranchs from the Indo-Pacific region leaves workers with a difficult set of taxonomic and nomenclatural problems to overcome as they attempt to sort out the relationships within this diverse family. Descriptions from the early 1800's through the mid 1900's lack consistency and are based primarily on external morphology, with only scattered references to important anatomical details. Subsequently, many species names have been synonomized, and other species have not been recorded since their original description. In some cases this may be due to the relative rarity of the taxa, in others the descriptions are insufficient to convince modern workers of their validity. Initial taxonomy was established by and expanded upon by Odhner (1936, 1963) but other workers still find difficulties with the most recent system (Willan 1988). Odhner proposed three plate bearing genera: *Marionia*, *Marioniopsis* and *Paratritonia*. His division was based primarily on characters of the digestive gland (liver), jaws and radula. *Marionia* was defined as having a digestive gland in two masses leaving the stomach uncovered, a jaw with 3 to 6 rows of fine denticles and a radula possessing tricuspid central teeth and differentiated first lateral teeth. *Marioniopsis* was defined by a digestive gland in a single mass covering the upper and left side of the stomach, jaws with a single row of strong denticles and a radula as in *Marionia*. In his 1963 key, Odhner defined *Paratritonia* as having a radula with unicuspidate central teeth and undifferentiated first laterals. This does not agree with the original description (Baba 1949), which stated that the first lateral teeth differ from the outer laterals. Baba also describes the jaw as having up to 10 rows of fine denticles, and a digestive gland in a single mass.

Odhner's classification scheme relies heavily on the morphology of the digestive gland, which he felt was of utmost importance in dividing the genera. This presents problems on more than one level. Firstly, the progression of the nudibranch digestive gland from a compact single mass to a divided state and then to a diffuse distribution is on a continuum, is not composed of discrete steps, and appears in multiple lineages. Secondly, detailed dissections of numerous tritoniids by the senior author have not always yielded results in agreement with published descriptions (e.g., Odhner 1963). In addition, there have been descriptions of new animals (e.g., Willan 1988) that do not fit well into any of the current genera, including the present study. Accordingly, the authors feel that it is most prudent for all new species of plate-bearing tritoniids to be placed in the genus *Marionia,* which precedes the more controversial genera *Paratritonia* and *Marioniopsis.*

Nudibranchs of the family Tritoniidae are thus far known to feed exclusively on soft corals, sea pens, and gorgonians, but exact feeding patterns are unknown for many species (McDonald and Nybakken 1999). The gut contents of *Marionia bathycarolinensis* sp. nov. contained skeletal elements of an undescribed octocoral of the genus *Paracis* Kükenthal, 1919; Family Plexauridae Gray, 1859. This is the first record of a nudibranch feeding on this genus of octocoral.

METHODS

Dissection was performed by a ventral incision through the length of the sole of the foot and around the genital and anal openings, allowing the removal of the entire visceral mass in one piece. The jaws and radula were freed from the buccal mass by partially dissolving tissues in 10% KOH solution. They were then rinsed in deionized water, air dried, mounted and coated for electron microscopy. Scanning electron micrographs (SEMs) were produced with a Hitachi S-520 or Leo 1450VP scanning electron microscope. Digestive contents were treated with undiluted household bleach to dissolve the tissue from the octocoral skeletal elements. After multiple rinses in water and 75% EtOH, sclerites and axial samples were mounted, dried and coated for electron microscopy. Slides of sclerites were also prepared for optical microscopy.

SPECIES DESCRIPTION

Suborder Dendronotacea Odhner, 1934
Family Tritoniidae Lamarck, 1809

Genus *Marionia* Vayssière, 1877

TYPE SPECIES: *Marionia berghi* Vayssière, 1877

Marionia bathycarolinensis Smith and Gosliner, sp. nov.

(Figs. 1–9)

TYPE MATERIAL.— All material examined was collected by the Coral Reef Research Foundation (CRRF) and has been deposited at California Academy of Sciences Department of Invertebrate Zoology (CASIZ). HOLOTYPE: CASIZ 156081, one specimen collected at 191.4 m depth, on rock, Mutremdiu 3, Palau, Caroline Islands, 07°16.27′N, 134°34.37′E, 18 March, 2001, L.J. Bell aboard the Deep Worker Submarine, dissected. PARATYPE: CASIZ 156082, buccal mass only, remainder of body not sent, Mutremdiu 3, Palau, Caroline Islands, 07°16.27′N, 134°34.37′E, 25 March, 2001, P.L. Colin aboard the Deep Worker Submarine, 222.5 m depth, on rock, dissected.

EXTERNAL ANATOMY.— The size of the living paratype specimen was approximately 118 mm in length. Only the buccal mass of this specimen was sent. The color of the living animal (Fig. 1a) is brick red, with scattered patches of lighter red and greenish-red on the notum. There are also small white flecks, patches, and short linear white markings on the body. The sheaths and shafts of the rhinophores are brick red, with the apical portions a contrasting dark greenish-red color. The preserved holotype specimen is 155 mm in length, and 65 mm wide by 40 mm high in its largest section. The size of this animal alive was not recorded. The notum is a dull red color, with patches of a greenish tinge. The sides are of a more even red color. The foot, rhinophores and branchial plumes all have a greenish tinge. The body is elongate, subquadrilateral in cross section, with the largest section at about ⅔ of the way to the posterior end of the foot. The tapering posterior of the notum overhangs the posterior end of the foot by about 20 mm. The broad oral veil is slightly incised at midpoint and extends about 5 mm beyond the front of the body. There are 12 velar papillae on each side of the veil. The relatively short velar papillae are arranged in multifid groups, with blunt rounded apices. The grooved oral tentacles usually associated with the tritoniids are present but are not distinctly demarcated, instead being incorporated as the outer margins of the veil. The body is finely granular all over, except for the smooth sole of the foot, with some development of low rounded tubercles on the notum and sides. The broad foot is rounded anteriorly. From the narrowly overhanging margin of the notum are produced the rhinophores and branchial plumes. In the holotype, the rhinophoral shafts are completely retracted into widely spaced, 6 mm-long sheaths. The photograph of the living animal (Fig. 1a) shows a typical tritoniid arrangement, with a central clavus surrounded by a series of pinnate projections. The branchial plumes are relatively short, the largest being slightly greater in length than the extended rhinophores in the photograph. The anterior 8 or so plumes are discrete and easy to count, whereas the more posterior plumes tend to run together, making an exact count difficult. There are approximately 22 plumes per side, with the largest in the middle third of the body. The branchial plumes are divided into three or four main branches, which then subdivide one or two more times. The gonopore is located on the right side, at about midline below and between the 4th and 5th branchial plume. It has the three-valve appearance of some tri-

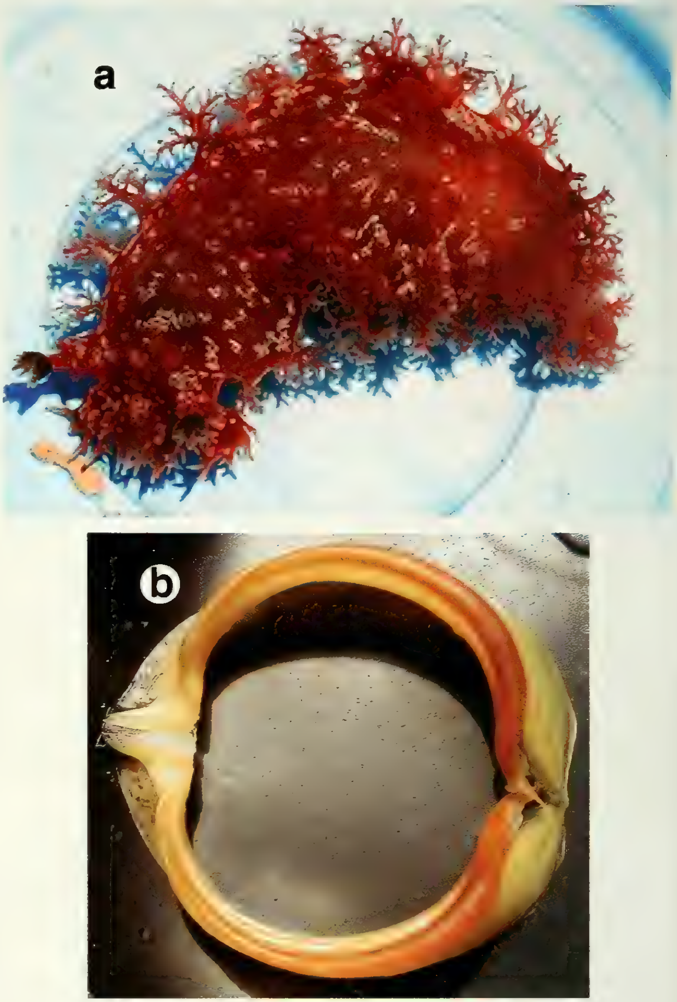

FIGURE 1. *Marionia bathycarolinensis* sp. nov., digital photographs. (a). Photo of living animal provided by CRRF. (b). Jaws of paratype, 35 mm in length.

toniids, and the tip of the penial papilla was visible. A floret of distended tissue surrounds the large opening of the anus, which is situated close to the notal margin below the 10th and 11th branchial plume on the right. The nephroproct opens between the 8th and 9th plume, just anterior to the anus.

Digestive System.— The jaws are yellowish brown in color, with a darker, thickened reddish brown masticatory margin slightly overhanging the length of the base (Fig. 1b). The masticatory margin appears smooth to the naked eye, but scanning electron microscopy reveals the presence of 25 or more rows of jaw rodlets visible in approximately the distal 5 mm of the half jaw examined (Figs. 2–3). The jaw rodlets exhibit a complex ultrastructure, with multiple vertical elements encased in an outer layer showing horizontal sculpture. The radula of the paratype is large compared with other tritoniids, with a formula of 72 (142.1.1.142) at its broadest point (Figs. 4a-d, 5a–b). The base of the rachidian is roughly rectangular, and is wider than it is long. The upper margin of the base (as oriented in the figures) is incised in the shape of a 'V'. The central cusp arises as a sturdy wedge-shaped process oriented nearly 90° from the plane of the base. The top of the wedge flattens and forms a long, emarginate, blade-shaped triangular denticle. Behind the base of this denticle the top of the wedge forms two projecting ridges that follow the 'V' shape of the margin. The rows of teeth are arranged very closely together, so that the projecting wedge of the central cusp fits neatly into the 'V' shaped margin and ridges of the next tooth, with the apex of the flat blade extending over the top. At the base of each wedge-shaped ridge is a small, flattened, emarginate denticle, considered here as accessory. The two outer cusps of the rachidian are shorter than the median, and are formed from the thickened outer margins of the base. Their surface and that of the accessory denticles bears a pattern of folds or ridges resembling the veins on a leaf. The

Figure 2. SEMs of jaw of paratype. (a). Proximal portion of masticatory border showing eruption of jaw rodlets. (b). Distal portion of masticatory border, showing part of overhang broken off in preparation. (c). Higher magnification view of proximal masticatory border. (d). Close up of rodlets in proximal masticatory border.

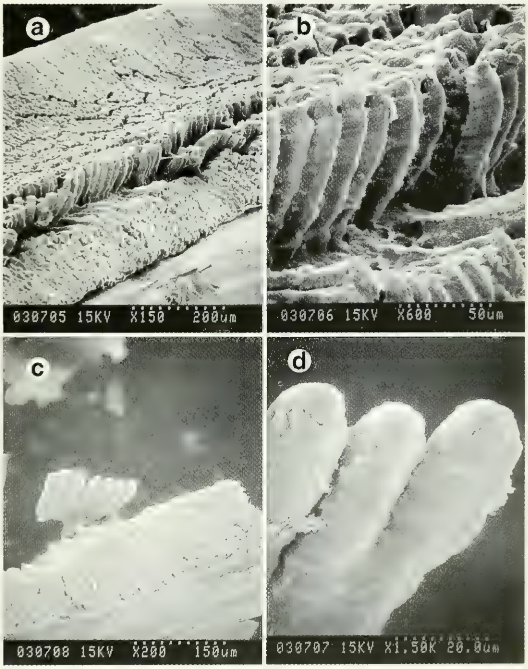

Figure 3. SEMs of jaw of paratype. (a). View of rodlets near distal end of masticatory border. (b). Detail of rodlets from same area. (c). View of rodlets at distal end of masticatory border. (d). Detail of rodlets seen in Figure 3c.

first lateral teeth are differentiated from the remaining laterals, being more heavily constructed with a short, hooked, chisel-shaped denticle fitting closely with the edges of the outer cusps of the rachidian. The remaining laterals are straight to slightly curved, and relatively broad and stout (Figs. 5 a–b). A pair of floccose salivary glands extended backwards from the proximal portion of the buccal mass, with attachments to the buccal mass on either side of the esophagus. The preserved salivary glands exhibit a greenish coloration. The esophagus extends about 8 cm from the median posterior buccal mass as a long straight tube, widening into a distended sac-like portion before turning and entering the stomach on the ventral side (Fig. 5c). A large bolus of gorgonian food material was present in the proximal esophagus, and will be described and discussed in a later section. The stomach is relatively small, 2 cm in diameter, with a muscular girdle visible in the proximal portion (Fig. 5c). Inside the stomach are approximately 50 stout, dark brown plates arranged so that the bases are attached to the muscular girdle and the plates point to the lumen of the stomach (Figs. 6a–b). The plates are roughly rectangular, with the exposed corners rounded, and most are about 7 mm long by 3mm high. A pair of larger, thicker and higher plates surrounds the typhlosole that continues through the stomach from the esophagus and into the intestine. There are also some thinner plates and some plates that are only 4 mm long interspersed in no discernable pattern. The intestine (Fig. 5c) exits the stomach from the anterior left portion, curving up and around the anterior portion of the digestive gland towards the right, becoming wider for a portion before narrowing again to terminate at the anus. The compact digestive gland is divided into two lobes, each with a duct leading into the stomach. The large, spheroid posterior portion has an anterior hollow that fits around the posterior stomach, leaving the top exposed. The smaller anterior

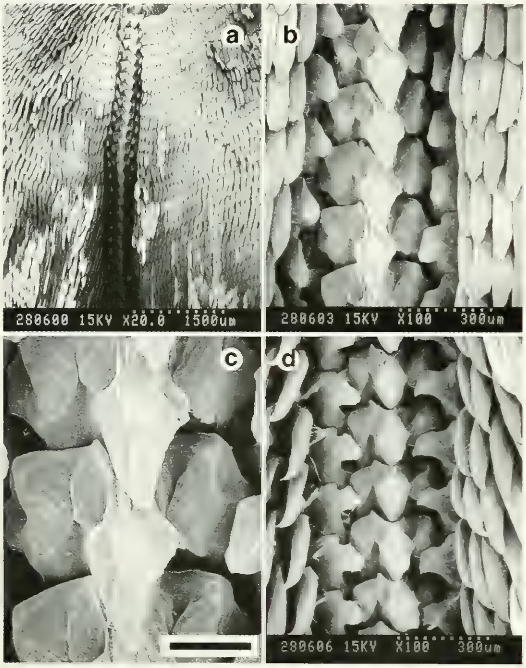

FIGURE 4. SEMs of radula of paratype. (a). Low magnification view of radula, older portion. (b). Rachidian teeth, first and inner lateral teeth at older portion. (c). Detailed view of rachidian at area shown in Figure 4b. Scale bar = 300 µm. (d). Rachidian teeth, first and inner lateral teeth at newer portion.

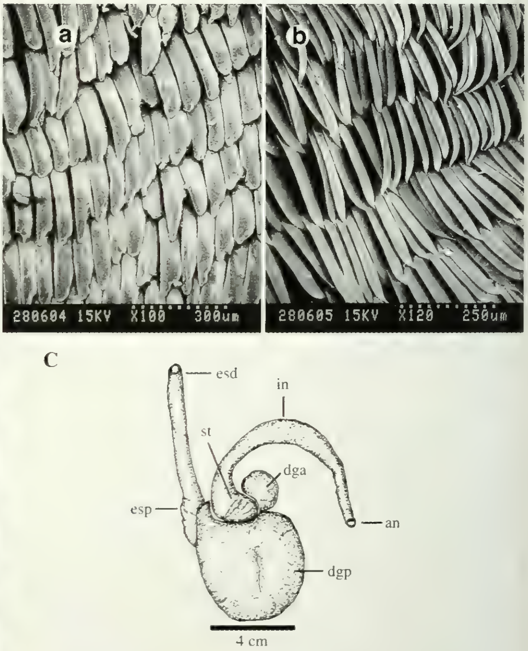

FIGURE 5. SEMs from paratype, drawing from holotype. (a). Middle latteral teeth from older portion of radula. (b). Outer laterals from newer portion of radula. (c). Visceral mass (from holotype). an = anus; dga = anterior digestive gland; dgp = posterior digestive gland; esd = distal esophagus; esp = proximal esophagus; in = intestine; st = stomach.

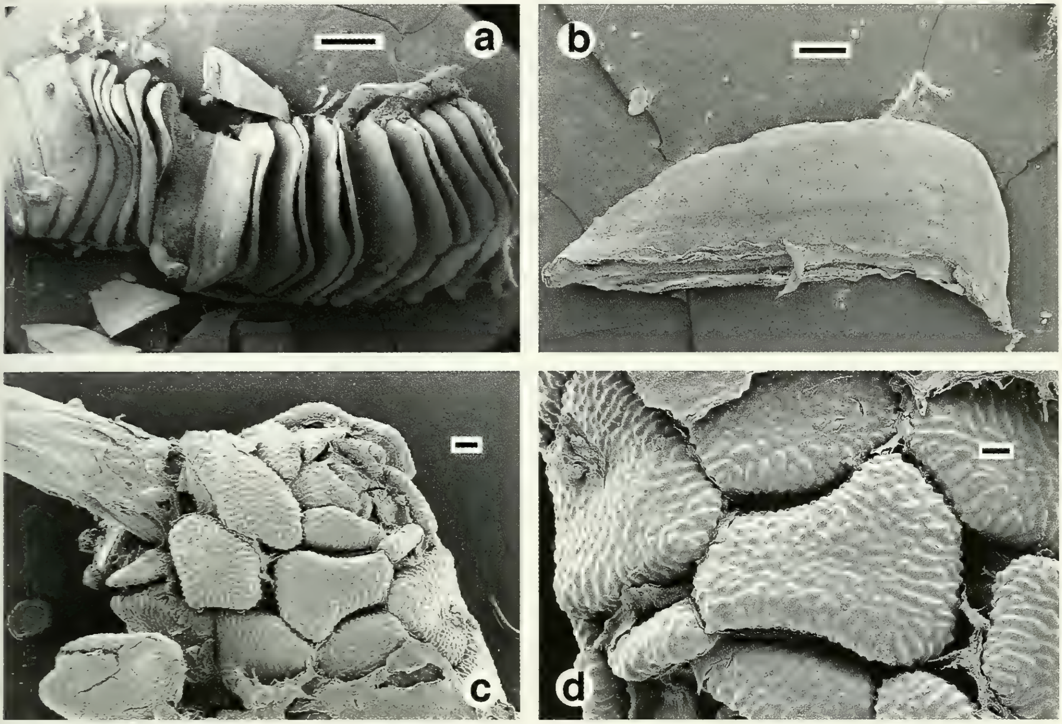

FIGURE 6. SEMs from holotype. (a). Portion of band of stomach plates, showing typhlosole area. Scale = 1 mm. (b). Isolated plate. Scale = 400 µm. (c). Portion of gut contents, showing overview of characteristic plates and 'woody' stem. Scale = 200 µm. (d). Closer view of plates. Scale = 100 µm.

lobe abuts the right anterior portion of the stomach, and is loosely connected to the posterior digestive gland (Fig. 5c).

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic. The diffuse ovotestis covers much of the surface of the digestive glands. A narrow hermaphroditic duct connects to the narrow end of the ampulla (Fig. 7a). The ampulla is muscular and convoluted, its wide end encased within the compact female gland mass. The smaller albumen gland is easily discernable from the larger membrane and mucos glands. The proximal vas deferens emerges from the female gland mass as a thin, relatively straight tube for about 10 mm, becoming thickened and sinuous in its median portion. The distal portion then extends, thinning slightly before entering the base of the conical unarmed penis, lying near the gonopore. The muscular bursa copulatrix is an inflated oval 18 mm long. The vaginal duct is approximately equal to the bursa in length, widening at the vaginal atrium. The oviduct exits the female gland mass and opens to the vaginal atrium.

NERVOUS SYSTEM.— The ganglia of the central nervous system sit on the dorsal esophagus, just behind the buccal mass (Fig. 7c). A thin transparent membrane not apparent in dissections of other tritoniids covers the ganglia and large nerves. The paired cerebral and pleural ganglia are distinct but somewhat fused, and the pairs are joined by a short connective. The pedal ganglia are on either side of the cerebropleurals, joined to them by short connectives, and to each other by the circum-esophageal nerve ring, which also contains commisures joining the cerebropleurals. A pair of buccal ganglia is present on the ventral esophagus, just anterior to the nerve ring. These are joined by a short connective (Fig 7c). The central nervous system and buccal ganglia are distinctly asymmetrical and 'lumpy' in appearance, with irregular nodules and distinct giant nerve cells scattered about. The darkly pigmented eyes are small, connected to the central nervous system by long nerves.

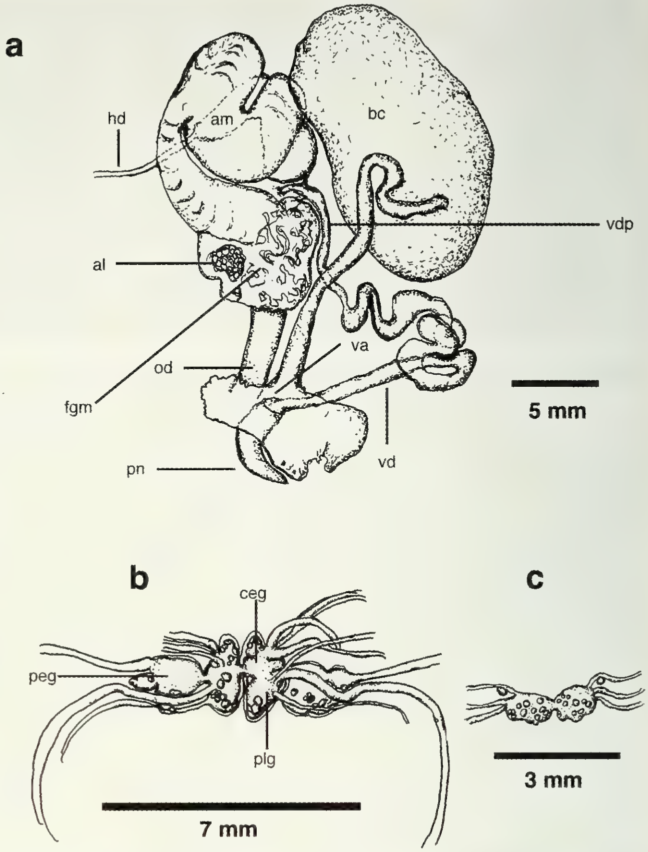

FIGURE 7. Drawings from holotype. (a). Reproductive system. Al = albumin gland; am = ampulla; bc = bursa copulatrix; fgm = female gland mass; hd = hermaphroditic duct; od = oviduct; pn = penis; va = vaginal atrium; vd = distal portion of vas deferens; vdp = proximal portion of vas deferens. (b). Central nervous system. ceg = cerebral ganglia; peg = pedal ganglia; plg = pleural ganglia. (c) Buccal ganglia. Scale bars as indicated.

GUT CONTENTS.— The contents of the digestive system contained both free sclerites and large pieces consisting of a "woody" appearing axis which is covered by distinctive large plates (Figs. 6c–d; 8a–d; 9a–b). The exposed sides of the plates have a pearly appearance, the bumpy surface giving the impression of sclerites immersed in a smooth nacreous coating. There is a distinct transition between the smooth exposed side and the rougher surface of the attached side. A crack in the membrane of the attached side shows a few sclerite-like objects imbedded in a matrix. Although it is not possible to know with any certainty the origin or exact identity of the octocoral from which the free sclerites were derived, the larger pieces are consistent with the genus *Paracis* Kükenthal, 1919, Family Plexauridae Gray, 1859 and appear to belong to an undetermined species (G.C. Williams, pers. commun.). Further references to octocoral information and biology can be found in Smith and Gosliner (2003).

DISTRIBUTION.— *Marionia bathycarolinensis* sp. nov. is known only from the type locality of Palau, in the Caroline Islands.

ETYMOLOGY.— The first part of the specific name is derived from the Greek, *bathys* (deep); the latter part refers to the type locality in the western-most fringe of the Caroline Islands.

DISCUSSION

In two recent papers (Avila et al. 1999; Jensen 1994), the anatomical and morphological characters of plate-bearing tritoniids have been tabulated. Avila et al. compared characteristics of species of the genus *Marioniopsis*, and included eight other species along with their newly described species. Jensen compared anatomical characters of species of *Marionia* and *Marioniopsis*, listing 17 species plus her newly described species. The combined species discussed

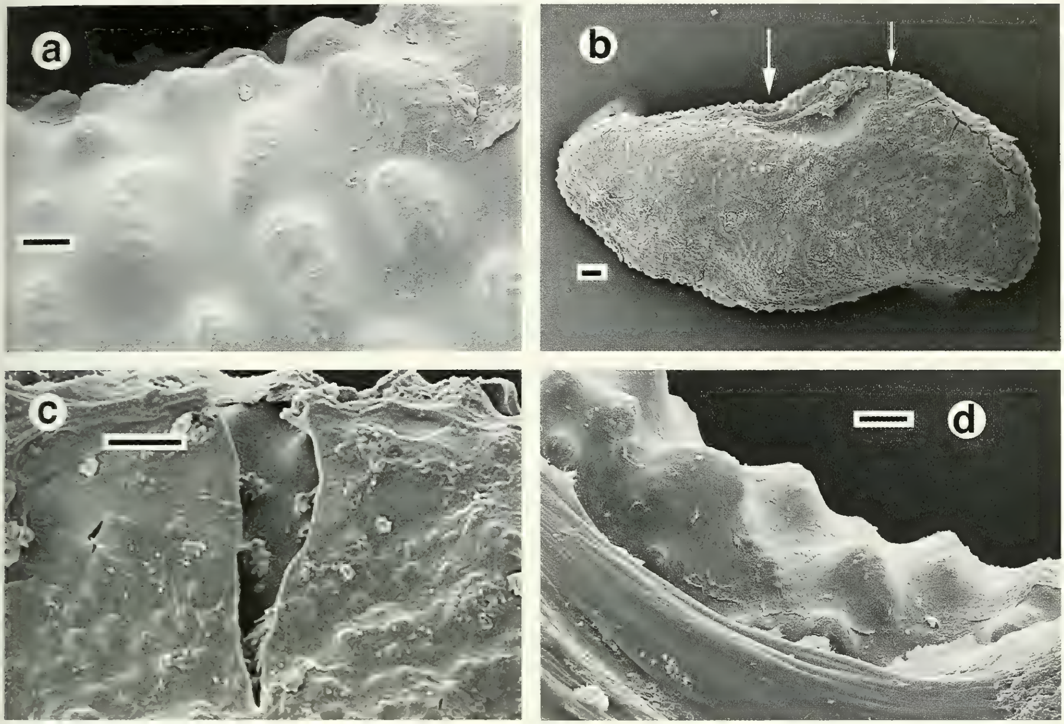

FIGURE 8. Detailed view of detached octocoral plate. (a). Close up view of exposed (front) side. Scale bar = 20 µm (b). A single detached plate, viewed from the attachment (back) side. Scale bar = 100 µm. Small arrow indicates area detailed in 8c, large arrow indicates area detailed in 8d. (c). Detailed view of area indicated by smaller arrow in 8b. Scale bar = 100 µm. (d). Detailed view of area indicated by larger arrow in 8b. Scale bar = 20 µm.

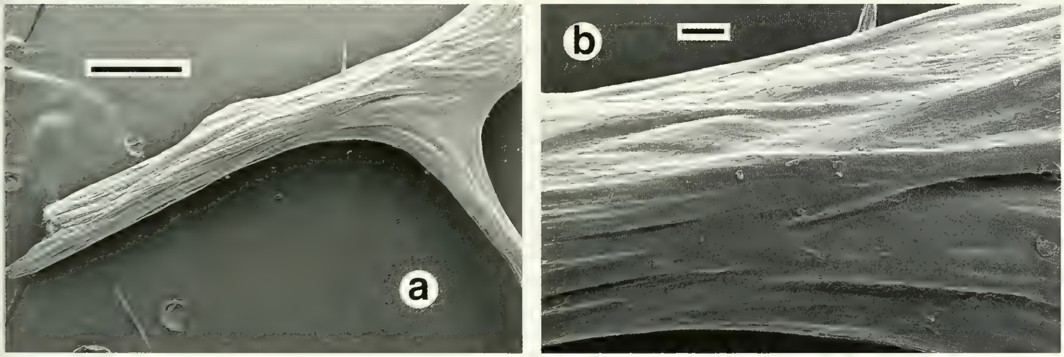

FIGURE 9. A Portion of the 'woody' axis of the octocoral. (a). Scale bar = 1 mm. (b). Scale bar = 100 µm.

in both papers are summarized in Table 1, along with *Paratritonia lutea* Baba, 1949, and *Marionia bathycarolinensis* sp. nov.

There are two external characters that differentiate all other plate-bearing tritoniids from *Marionia bathycarolinensis* sp. nov.: the number of branchial plumes and the number of velar papillae. *Marionia bathycarolinensis* sp. nov. has 22 pairs of branchial plumes and 12 pairs of compound velar papillae. All other species listed have 16 or fewer branchial plumes, with the excep-

TABLE 1. Comparison of Indo-Pacific species of the genus *Marionia*

Species	*Branchial plumes*	*Velar papillae*	*Jaws*	*½ row of radula teeth*	*Stomach plates*
M. albotuberculata	9 pairs	5 pairs, some compound	1 row of teeth, trace of second	95	>100
M. babai	7 pairs	6 pairs, compound	> 100 teeth, number of rows not stated	25	present
M. blainvillea	10–12 pairs	7 pairs	2–4 rows of teeth	15–21	ca 40
M. chloanthes	9+ pairs	4 pairs, some compound	5–6 rows of teeth	22	70
M. cucullata	12–16 pairs	7–11 pairs	6 rows of teeth	58	30–40
M. cyanobranchiata	9–13 pairs	4–7 pairs, simple	1 row of teeth, trace of second	15–50	100–120
M. dakini	13 pairs	6–7 pairs, compound	1 row of 45 teeth	135	present
M. echinomuriceae	10–14 pairs	6–8 pairs	1 row of teeth, indistinct	65	28
M. fulvicola	7–9 pairs	3–4 pairs, most simple	4–5 rows,>100 teeth	38–42	22–32
M. granularis	13–14 pairs	6 pairs	unknown	50	present
M. levis	9–10 pairs	3–5 pairs, compound	1–3 rows, 14-30 teeth	80–130	ca 150
M. pambanensis	12 pairs	6 pairs	unknown	43	present
M. pellucida	13 pairs	6 pairs	unknown	22	70
M. platyctena	100 pairs	5–7 pairs, simple	10 rows of teeth	71–103	30–35
M. putulasa	15 pairs	6 pairs	unknown	112	25
M. rubra	10–12 pairs	6 pairs, compound	1 row of 100-120 teeth	50–55	present
M. tessellata	13 pairs	7 pairs	3 rows of teeth	unknown	present
M. bathycarolinensis	22 pairs	12 pairs, compound	25–100 rows of rodlets	142	50
M. viridescens	10 pairs	7 pairs, some compound	single row of teeth	90	25
M. olivacea	9–15 pairs	7 pairs, some compound	3–7 row of teeth	70–80	50–60
Paratritonia lutea	6–7 pairs	3–4 pairs	3–10 rows of teeth	110	25

tion of *M. platyctena*, which has 100. However, this animal is recorded as having a jaw with 10 rows of teeth, a velum with 5–7 pairs of simple papillae, a radular half-row of up to 103 lateral teeth and a maximum of 35 stomach plates. This is in contrast with *M. bathycarolinensis* sp. nov., which has a jaw armed with rodlets, a velum with 12 pairs of compound papillae, a radula with a half-row of 143 lateral teeth, and 50 stomach plates. Only *M. cucullata* (which may be a synonym for *M. blainvillea)* has a recorded number of velar papillae approaching that of the new species. However, *M. cucullata* does not match our new species in any of the other characters discussed, differing in the number of branchial plumes, jaw morphology, radular formula and number of stomach plates.

Internally, the principal apomorphy of *Marionia bathycarolinensis* sp. nov. is a jaw armed with multiple rows of rodlets. This type of denticulation has not been recorded for any other species of tritoniid nudibranch.

The basic form of the tritoniid radula is, with few exceptions, consistent throughout the genera, consisting of a tricuspid central tooth flanked by a pair of first lateral teeth differentiated from the remaining curved outer laterals. The species described here does not differ from the basic form, but is distinctive in the appearance of the central tooth. The median cusp is elongate, overlapping the next row when the radula is contracted. The leaf-like shape of this flattened central cusp has not been recorded for any other species of tritoniid.

The remaining distinguishing characters are more general: large size and a relatively compact visceral mass with an elongate esophagus. Body lengths of over 10 cm are at the large end of the tritoniid size continuum, mostly occurring in temperate species without stomach plates. Both specimens described here are of this large size. Figure 5b illustrates the long straight esophagus and relatively compact visceral mass, which contrasts with published drawings of other tritoniids (Odhner 1936) and the personal observations of the present authors.

ACKNOWLEDGEMENTS

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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Perulibatrachus aquilonarius, a New Toadfish Species from India (Teleostei: Batrachoididae)

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The fourth known species in the genus *Perulibatrachus* is described. It is the northernmost species in the genus, and the second known from the Indian Ocean. It has a wider head than the other described species and differs from others in counts: dorsal-fin elements III-17, anal-fin rays 13, pectoral-fin rays 21, vertebrae 26. It has a shallow, funnel-shaped pocket in the pectoral-fin axil.

The genus *Perulibatrachus* is currently represented by three species. Two species are known only from the west coast of Africa: *P. elminensis* (Bleeker, 1863) from Ghana south to Walvis Bay, Nambia, and *P. rossignoli* (Roux, 1957) from Gabon south to Walvis Bay (Roux 1981; Hutchins 1986). A third species, *P. kilburni* Greenfield, 1996, is known only from Natal, southeastern South Africa. In 1941, A.W.C.T. Herre collected a toadfish specimen, purportedly in India, which he or someone else had identified as *Chatrabus damaranus*. The specimen had been deposited in the ichthyological collections of Stanford University and later transferred to the California Academy of Sciences along with the rest of Stanford's collections. Recently, I found the specimen on the shelves at the Academy and on examination discovered that it does not belong to the genus *Chatrabus* but to the genus *Perulibatrachus*. The genus *Chatrabus* was described by Smith in 1949, whereas *Perulibatrachus* was not described by Roux and Whitley until 1972. Thus, at the time of its identification, *Chatrabus* would have been a logical choice in which to place this specimen.

The most recent key to toadfish genera is that of Smith (1952). In that key, *Perulibatrachus* would fall in section BIII, which includes *Chatrabus*, *Barchatus*, *Tharbacus*, *Batrachoides*, and *Halobatrachus*. Hutchins (1986) considers *Tharbacus* to be a synonym of *Chatrabus*. Roux (1981) presents a key to separate *Perulibatrachus* from *Halobatrachus*, which has a distinct foramen (axillary pore) on the upper part of the pectoral-fin axil, whereas the other genera have only a funnel-shaped pocket (*Perulibatrachus*) or neither a foramen nor pocket (*Chatrabus* and *Batrachoides*). In species without the pocket, the skin stretches straight across the pectoral-fin axil, whereas in *Perulibatrachus* there is a clear indentation, which is shallow in *P. rossignoli* or relatively deep in both *P. elminensis* and *P. kilburni*. The specimen from India has three dorsal-fin spines and two subopercular spines, placing it in the subfamily Batrachoidinae. The body is mostly scaled, it lacks a foramen in the pectoral-fin axil, and it has a shallow funnel-shaped pocket in the pectoral-fin axil, placing it in the genus *Perulibatrachus*.

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MATERIALS AND METHODS

All counts and measurements follow Hubbs and Lagler (1964) except that the last two fin rays are not counted as one unless it is clear that they are joined at the base. Measurements were made to the nearest 0.1 mm using dial calipers. All measurements are expressed as percentage of standard length (SL). Counts were made from a radiograph. Neither the holotype nor any additional material of *P. rossignoli* could be located at the Museum National d'Histoire Naturelle, Paris, by M.L. Bauchout and J.E. Randall, so comparisons with that species are based on the literature. Institutional abbreviations are as listed in Leviton et al. (1985).

SPECIES DESCRIPTION

Perulibatrachus aquilonarius **Greenfield, sp. nov.**

(Figs. 1A–B)

MATERIAL EXAMINED.— HOLOTYPE: CAS-SU 41322, 191.4 mm SL, India, Tamil Nadu State, Ennur Fisheries Station, Madras, January, 1941, A.W.T.C. Herre. ADDITIONAL MATERIAL EXAMINED: *Perulibatrachus kilburni*, RUSI 28203 (1; 56.6 mm SL). *Perulibatrachus elminensis*, MNHN 1967-909 (1; 204 mm SL), MNHN 1970-43 (1; 150 mm SL; cleared and stained).

DIAGNOSIS.— A species of *Perulibatrachus* with a wide head (43.6% SL), 17 dorsal-fin rays, 13 anal-fin rays, 21 pectoral-fin rays, 26 vertebrae, and a shallow, funnel-shaped pocket in the pectoral-fin axil.

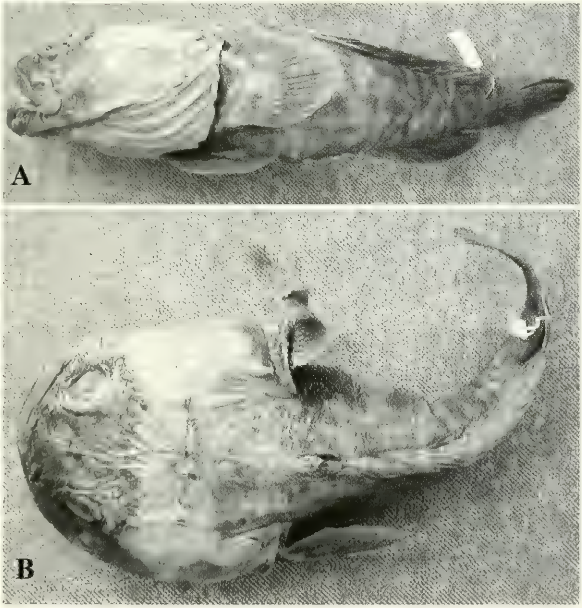

FIGURE 1. Holotype of *Perulibatrachus aquilonarius*, CAS-SU 41322. A. lateral view; B. dorsal view.

DESCRIPTION.— Dorsal-fin elements III-17; anal-fin rays 13; pectoral-fin rays 21; vertebrae 26; head length 45.0; head width 43.6; head depth 25.3; bony interorbital width 9.5; orbit diameter 7.6; snout length 8.8; upper jaw length 25.9; mouth width at rictus 36.1; first predorsal-fin distance 42.1; second predorsal-fin distance 61.6; preanal-fin distance 72.5; greatest body depth 25.2; caudal-peduncle depth 9.8; caudal-peduncle length 13.6; first dorsal-fin base length 11.4; second dorsal-fin base length 39.6; anal-fin base length 21.5; caudal-fin length 22.7; pectoral-fin length 25.0; pelvic-fin length 26.7; distance between pelvic-fin bases 15.3.

Head moderately depressed and wide, eyes medium in size and not raised above head profile. Pectoral-fin axil with a shallow, funnel-shaped pouch in upper half, glandular tissue present in rest of axil and on sides under pectoral fins. Some glandular tissue present on inner surface of pectoral fins. Body with small scales extending from middle of first dorsal fin back to caudal-fin base. Scales extending forward on ventral surface to pelvic fins. Two lateral lines: the upper one originating above upper opercular spine, running posteriorly in a straight line to below second dorsal-fin origin where it curves up to run along dorsal-fin base to its end, with about 41 pores present, each with two short skin flaps; the second lateral line, with about 17 pores, runs along anal-fin base. Vomer and palatine each with single row of slightly curved conical teeth. Dentary laterally with single row of conical teeth, double row near symphysis. Premaxilla with single row of conical teeth posteriorly, double row anteriorly. Subopercle with two spines. Anterior nostrils tubular; nostril on left side with a simple major tentacle; nostril on right side with three terminal tentacles; a cluster of multifid cirri surrounds each tubular nostril. Cirrus at distal end of maxilla with many tips. Ventral margin of dentary with numerous cirri. Dorsal surface of neurocranium completely covered with muscles, no exposed bone.

Color in alcohol: After 64 years in preservative, general background color is cream, overlaid with rusty brown pigment pattern. Anterior portion of head from posterior margin of eyes forward rusty brown. A cream band running from posterior margins of eyes posteriorly to opercular spine forms a distinct band across the head. The area posterior to this and extending back to first dorsal-fin origin overlaid with distinct, small, rust-colored spots. Sides of body, second dorsal fin, anal fin, pectoral, and caudal fins with scattered, irregular rust-colored spots. Ventral surface of head cream, area from pelvic fins posteriorly to anal-fin origin rust.

ETYMOLOGY.— The specific epithet is an adjective from the Latin, *aquilonarius*, meaning northern, referring the fact that this species has the northernmost distribution of any member of the genus *Perulibatrachus*.

COMPARISONS.— *Perulibatrachus aquilonarius* differs from all other species in the genus by having a wider head: 43.6 versus 29.7 in *P. kilburni*, 29.1–37.9 in *P elminensis*, and 37.8–40.9 in *P. rossignoli*. It differs from *P. rossignoli* by having 17 versus 19 second dorsal-fin rays, 21 versus 23 pectoral-fin rays, and 26 versus 29 vertebrae. It differs from *P. elminensis* by having 13 versus 14–17 anal-fin rays, 21 versus 26 pectoral-fin rays, and 26 versus 27–28 vertebrae. It differs from *P. kilburni* by having 17 versus 18 dorsal-fin rays, 13 versus 14 anal-fin rays, and 21 versus 19 pectoral-fin rays. It has a shallow, funnel-shaped axillary pocket, whereas it is deep in *P. elminensis* and *P. kilburni*.

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Brotula flaviviridis, a New Species of *Brotula* from Fiji (Teleostei: Ophidiidae: Brotulinae)

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The third known species of *Brotula* from the Indo-Pacific, *B. flaviviridis* sp. nov., is described from Fiji. *Brotula townsendi* is an antiequitorial species, known from the Hawaiian Islands, Johnston Island, and the Marshall Islands in the northern hemisphere, and Chesterfield Islands, New Caledonia, Loyalty Islands, Vanuatu, and Tonga in the southern hemisphere. *Brotula multibarbata* is widespread in the Indo-Pacific. *Brotula flaviviridis* differs from both in coloration, being yellow-green. It is similar to *B. townsendi* in having an eye that is narrower than the fleshy interorbital width, whereas *B. multibarbata* has an eye that is wider. It differs from *B. townsendi* by having a smaller eye and narrower interorbital width.

While conducting a survey of the marine fishes of Fiji, two specimens of a yellow-green brotula were collected using rotenone at the barrier reef on the north side of Kanacea Island in the Northern Lau Group, Fiji. The fresh coloration of these specimens was distinctly different from the other two species in the genus *Brotula* known from the Indo-Pacific.

The new species is placed in the genus *Brotula* because: the anterior nostril is well above the upper lip, near the eye; the supramaxilla is present; the dorsal-fin rays are equal to or longer than opposing anal-fin rays; and six barbels are present on the snout and six on the chin.

Only five species in the genus *Brotula* are currently considered to be valid. *Brotula barbata* (Bloch *in* Bloch and Schneider, 1801) occurs in the tropical and subtropical Atlantic Ocean. *Brotula clarkae* Hubbs (1944) occurs in the tropical eastern Pacific from the Gulf of California to Peru, and *B. ordwayi* Hildebrand and Barton (1949) occurs at Peru and the Galápagos Islands. In the Indo-Pacific Ocean, *B. townsendi* Fowler (1900) is known from the Hawaiian Islands, Johnston Island, Marshall Islands, Chesterfield Islands, New Caledonia, Loyalty Islands, Vanuatu, and Tonga, and *B. multibarbata* Temminck and Schlegel (1846) is widespread. Hubbs (1944) listed ten other described species as synonyms of *B. multibarbata*, and these were also listed by Nielsen, et al. (1999).

MATERIALS AND METHODS

Information on the holotype is presented first, followed by that of the paratype in parentheses. The paratype died with its mouth open wide, making measurements less accurate than those for the holotype. All measurements are presented as percentage of standard length (SL), and some as percentages of other body parts. Information on *Brotula clarkae* and *B. ordwayi* is from Allen and

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Robertson (1994) and Hubbs (1944). Pectoral-fin ray counts were obtained by slitting the skin on the inside of the right pectoral fin. Other fin-ray counts and vertebral counts were obtained from radiographs. Methods of counting and measuring follow Nielsen et al. (1999), and the format of the description follows Cohen and Nielsen (1982).

SPECIES DESCRIPTION

Brotula flaviviridis Greenfield, sp. nov.

(Figs. 1–3)

MATERIAL EXAMINED.— HOLOTYPE: CAS 221531, 125.0 SL, Fiji, Northern Lau Group, north side of Kanacea Island at copra plantation, 17°14.890′S, 179°08.475′W, isolated piece of barrier reef, sand and dead coral, 7–9.5 m, 5 January 2003, field number G03-15, rotenone, collected by D.W. Greenfield, K.R. Longenecker, and R.C. Langston. PARATYPE: CAS 221532, 151.0 SL, Fiji, Northern Lau Group, north side of Kanacea Island at copra plantation, 17°14.890′S, 179°08,475′W, overhang on barrier reef with sand at base, 12–14 m, 4 January 2003, field number G03-11, rotenone, collected by D.W. Greenfield, K.R. Longenecker, R.C. Langston, and Bio Koroi Mataitini. ADDITIONAL MATERIAL EXAMINED: *Brotula townsendi*: Hawaiian Islands, Oahu-CAS 221533. Johnston Island-BPBM 33975 (2), BPBM 29609 (1), BPBM 34043 (1). Chesterfield Islands-BPBM 33794 (5). New Caledonia-BPBM 22550 (1). *Brotula multibarbata*: Hawaiian Islands, Oahu-CAS 78987 (5), CAS 78901 (2), CAS 210003 (4). Fiji-CAS 218868 (4), CAS 219394 (5), CAS 219404 (5), CAS 219405 (4).

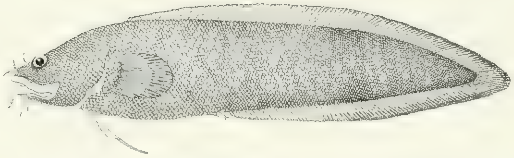

FIGURE 1. Drawing of holotype (CAS 221531) of *Brotula flaviviridis*.

FIGURE 2. Fresh color of holotype (CAS 221531) of *Brotula flaviviridis*. Photo D.W. Greenfield.

DIAGNOSIS.— A species of *Brotula* that is yellow-green in coloration, with an eye that is narrower than the interorbital width, 98–103 dorsal-fin rays, 77–79 anal-fin rays, 24 pectoral-fin rays, 43–44 vertebrae, 2–3 developed gill rakers, a fleshy interorbital width of less than 4.5 percent SL, and an orbit diameter 3.5 percent SL or less.

DESCRIPTION.— Dorsal-fin rays 97 (103). Anal-fin rays 77 (79). Pectoral-fin rays 24 (24). Vertebrae 12+32 = 44 (11+32 = 43). Total developed gill rakers 3 (2 one side, 3 other). Longitudinal scale series about 133. Predorsal length 26.6 (25.8). Preanal length 48.8 (48.3). Preventral length 14.2 (21.0). Body depth at vent 19.2 (21.5). Head length 22.3 (23.5). Eye diameter 3.2 (3.5). Snout length 4.6 (6.0). Fleshy-interorbital width 4.2 (3.8). Upper-jaw length 12.0 (13.8). Greatest maxillary width 9.7 (12.4). Pectoral-fin length 14.2 (13.8). Pectoral-fin peduncle width 6.6 (6.3). Ventral-fin length 20.3 (17.8).

Body deepest just before end of pectoral fin, tapering to tail, which is not greatly attenuate. Body scales relatively large for the genus, about 133 rows along the side of the body. Head covered with scales. Scales on belly forward to ventral fins. Scales present on pectoral-fin base and also out onto the dorsal and anal fins. Head compressed. Snout bluntly rounded, longer than orbit diameter. Upper lip terminal, extending slightly beyond lower jaw. Posterior nostril with raised rim, adjacent to anterior margin of eye. Anterior nostril immediately anterior to posterior nostril, with a raised rim and barbel on posterior margin. Two barbels at front of snout, one on each side of middle of snout. Another barbel on each side of snout, about at level of ventral margin of eye, for a total of six barbels on snout. Maxilla notably expanded posteriorly, reaching about one pupil diameter past rear margin of orbit. A sheath of tissue on upper third of maxilla, with a notch at end exposing top end of maxilla. Underside of lower jaw with six barbels, three on each side. Two pores at symphasis and one adjacent to posterior side of anteriormost barbel. Teeth small and granular, some with fine points, on dentary, premaxilla, palatine, and vomer. Vomerine tooth patch rounded anteriorly and V-shaped.

First gill arch with four (five) short, stubby rakers on upper arm, a longer (developed) raker at angle, lower arm with two (one) longer and ten (14) short protuberances. Longest raker about one-half eye diameter. Longest gill filament a little longer. Branchial cavity and palate pale.

Lateral line not obvious. Dorsal fin originating over end of pectoral-fin peduncle, at origin of pectoral-fin rays. Pectoral fin on a short, rounded, fleshy peduncle. Opercle with a strong spine hidden under skin which continues as a prominent flap of skin dorsal to pectoral-fin base. Ventral fins inserted well behind symphysis of cleithra, about under opercular spine. Lining of peritoneal cavity pale, with scattered, small, black spots. Stomach and intestine pale.

Color in alcohol: Background color cream, overlaid with gray-brown pigment on center of scales, leaving the scales outlined. Nape, snout, and front of jaws with greater concentration of gray-brown. Barbels and posterior ends of maxilla and premaxilla white. Ventral surface of head gray. Pectoral fins clear. Pelvic fins white. Bases of dorsal and anal fins gray where scales extend out onto them. Distal margin of anterior two-thirds of dorsal fin clear. Posterior third gray with black margin. Anal fin clear distally on anterior two-thirds of fin, posterior third like posterior part of dorsal fin. Caudal fin edged in black.

Color of fresh specimen: Background color yellow with a greenish tinge. Head yellow-green. Pupil of eye black, surrounded by yellow iris. Barbels on snout orange, barbels under chin white. Snout and tip of upper and lower jaws dusky. Anterior two-thirds of body primarily yellow-green, posterior third more dusky green. Belly yellow-white. Pectoral fin yellow. Anterior half of dorsal fin yellow with orange margin. Posterior half of dorsal fin reddish grading into black posteriorly as it merges with black caudal fin. Anal fin similar to posterior half of dorsal fin. Pelvic fins white.

ETYMOLOGY.— The specific epithet is a compound adjective, combining the Latin *flavus*, meaning golden-yellow, plus *viridis*, meaning green, alluding to the yellow-green color of the species.

COMPARISONS.— *Brotula flaviviridis* differs from all known valid Pacific Ocean species by its yellow-green coloration. It differs from the two eastern Pacific species, *B. clarkae* and *B. ordwayi*, by having fewer dorsal-fin rays, 97–103 versus 108–112 (*B. clarkae*) and 118–125 (*B. ordwayi*), and fewer anal-fin rays, 77–79 versus 78–89 (*B. clarkae*) and 86–94 (*B. ordwayi*). It also differs from *B. clarkae* in having 24 pectoral-fin rays verses 27–28. As pointed out by Hubbs (1944), "the distinction between the relatively large scales of the Indo-Pacific species and the small scales of the American ones, particularly of *B. clarkae*, was obvious at sight." *Brotula flaviviridis* differs from the Indo-Pacific species *B. multibarbata* by having an eye that is narrower than the interorbital width, verses one that is wider. It differs from the other Indo-Pacific species, *B. townsendi*, by having a smaller eye (3.5 % S.L. or less) and narrower interorbital width (3.8% S.L or less) (Fig. 3).

DISCUSSION.— Because one of the eleven species listed by Hubbs (1944) as a synonym of *B. multibartata*, *B. townsendi*, is valid, it was necessary to investigate the status of the other ten species because in many cases he worked only from the literature. Patrice Pruvost (MNHN) provided me with a photograph of the dried holotype (A.8468) of *Brotula burbonensis* Kaup (1858). It has a large eye that is typical of *B. multibarbata*, not the smaller eye of *B. flaviviridis*. The types

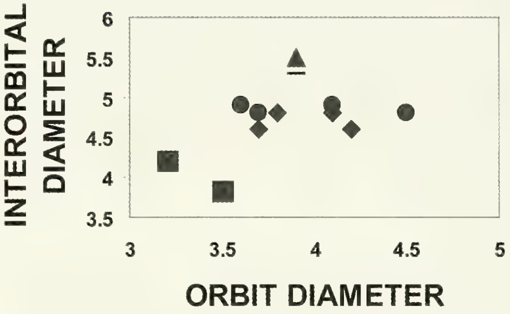

FIGURE 3. Interorbital diameter versus orbit diameter, both as percentage SL for *Brotula flaviviridis* (squares), and *B. townsendi* from Hawaiian Islands (triangle), Johnston Island (diamonds), New Caledonia (line), and Chesterfield Islands (circles).

of three species of Hubbs' synonyms are at the British Museum of Natural History: *B. ensiformis* Günther (1862) (stuffed syntypes) from Vanuatu, *B. jayakari* Günther (1909) (BMNH 1888.12.29.193) from Oman, and three syntypes of *B. mülleri* (corrected to *B. muelleri*) Günther (1909) (BMNH 1881.10.28.8 from Ponape, 1868.8.1.7 from Tahiti, and 1876.5.19.45 from Tahiti). In his description of *B. ensiformis*, Günther (1862) states "The width of the interorbital space is less than the horizontal diameter of the orbit," which clearly places it in *B. multibarbata*. Oliver Crimmen (BMNH) has kindly examined the types of these three species for me, and confirmed that *B. ensiformis*, and *B. jayakari* have the large eye typical of *B. multibarbata*. *Brotula muelleri* is represented by three syntypes and is a mixed type series, containing both large and small eyed species. In the original description, Günther stated that the width of the interorbital space is much smaller than the diameter of the eyes, which clearly places this species as a synonym of *B. multibarbata* as concluded by Hubbs (1944). To avoid further confusion, I am designating one of the syntypes, BM(NH)1876.5.19.45 from Tahiti, which has the large eye, as the lectotype of *B. muelleri*, and as such, it is a synonym of *B. multibarbata*. The other two syntypes, now paralectotypes of *B. muelleri*, have the small eye, typical of *B. townsendi* and *B. flaviviridis*.

Brotula palmietensis Smith (1935) (RUSI 299) from South Africa was listed as a synonym of *B. multibarbata* by Nielsen and Cohen (1986). *Brotula formosae* Jordan and Evermann (1902) (ZUMT 359) from Taiwan was listed as a synonym of *B. multibarbata* by Chen and Shao (1991). *Brotula japonica* Steindachner and Doderlein (1887) (NMW) from Japan was listed as a synonym of *B. multibarbata* by Lindberg and Krasyukova (1975) and also was not listed as a valid species in Nakabo (2002).

Two of the species were described from the Hawaiian Islands, *B. marginalis* Jenkins (1901) and *B. multicirrata* Vaillant and Sauvage (1875). Hubbs (1944) examined the type of *B. marginalis* at the USNM (49694) and found it to be *B. multibarbata* with a damaged tail. Both Fowler (1900) and Hubbs (1944) considered *B. multicirrata* to be a synonym of *B. multibarbata*. It was described as having eight rather than six barbels on the snout. Many individuals of *B. multibarbata* have been collected at the Hawaiian Islands and none have had eight barbels. Hubbs (1944) speculated that the nasal flap had been counted as a barbel. Considering that only two species of *Brotul*a are known from the well-collected Hawaiian Islands, and that *B. townsendi* is relatively rare, treating *B. multicirrata* as a synonym of *B. multibarbata* is justified.

Finally, *B. ferruginosus* (Tickell *in* Day, 1888) is not available (Eschmeyer 1998).

Brotula flaviviridis appears to be most similar to *B. townsendi*, which was previously known only from the Hawaiian Islands and Johnston Island but now is known to be antiequatorial. Randall (in press) lists its distribution as "Known from the Hawaiian Islands, Johnston Island, Marshall Islands, Tonga, Loyalty Islands, and Vanuatu." It is also known from the Chesterfield Islands and New Caledonia (this paper). *Brotula flaviviridis* shares the relatively small eyes with *B. townsendi*. and has similar counts. *Brotula townsendi* is an orange brown with a yellowish pectoral fin in fresh coloration. Two lots at the Bishop Museum from the South Pacific were identified as *B. townsendi*: BPBM 22550 from New Caledonia and BPBM 33794 from Chesterfied Islands in the

Coral Sea. Examination of these specimens confirmed that they appear to be conspecific with *B. townsendi*, clustering together in Figure 3. *Brotula townsendi* thus joins a number of other species from the Hawaiian Islands that demonstrate an antitropical or antiequatorial distribution (Randall, 1982). *Brotula flaviviridis* most likely was derived from these populations of *B. townsendi* to the southwest.

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Short Communications

First Record of the Eastern Atlantic Squirrelfish *Sargocentron hastatum* (Holocentridae) from the Western Atlantic Ocean.— Each summer a ReefNet team conducts a trip to a different Caribbean destination to survey marine life using film and video to document their sightings. In 2003 the team surveyed St. Vincent Island, and in 2004, San Andres, Colombia. At both of these sites the team observed and photographed a squirrelfish that they never had seen before. The results of this most recent trip to San Andres were made available on the web (*http://www.reefnet.ca*) and sent to the third author by e-mail. Upon viewing the photographs of this squirrelfish, the third author recognized it as *Sargocentron hastatum*, a distinctive species previously known only from the eastern Atlantic, where it has been recorded from Portugal southward to Angola, including the Cape Verde Islands.

At St. Vincent the squirrelfish was first seen at a location called the Bat Cave, a cavern with a swim-through, located on the west side of the island north of Kingstown. The fish was observed at 9.1 meters (Figs. 1–3). At a second site about 90 meters south of the first location, two more specimens were observed swimming upside-down along the ceiling of a smaller cave.

During dives along the southwest coast of San Andres, the team encountered cracks, caves, and caverns in the shallow water near shore, where craggy limestone drops steeply into the water. In two instances they sighted and attempted to photograph *S. hastatum*, and were successful in one case (Fig. 4). These fish also were at a depth of about 9.1 meters. All observed individuals were well back in a cave. The photographed fish was in the northeast corner of the cave that was about 9.1 meters wide, 1.2 meters high, and 6.1 meters deep. It was seen hiding from the dive lights among a few large rocks, was extremely shy, and would only reveal itself after a few minutes if the lights were turned off.

Sargocentron hastatum (Cuvier 1829), is easily recognized by the distinct, alternating, red and white lines on the entire side of the body, a dorsal fin with distinct white spots on the basal half of the membranes, a very long third anal-fin spine reaching, when folded back, to the caudal-fin base, and a very long spine on the opercle (Greenfield 1981, in prep.). In earlier literature this species was referred to as *Adioryx hastatus*.

The broad, deep-water region between the West African coast and the western tropical Atlantic is known as the Mid-Atlantic Barrier (Briggs 1974, 1995). Briggs (1974) calculated that for fishes, this barrier was 91 percent efficient in preventing transatlantic movement, and that the predominant migratory movement across this barrier is from west to east. He goes on to say that "The westward colonization traffic appears to be restricted to certain dominant species that originated in the Indo-West Pacific and then gained access to the Atlantic by rounding the Cape of Good Hope. So far, there are no indications that species originating in the eastern Atlantic, and belonging to genera typical of that area, have been successful in becoming established on the western side." Four holocentrid species are known from the eastern Atlantic Ocean, *Corniger spinosus, Holocentrus adscensionis, Myripristis jacobus*, and *Sargocentron hastatum*. All of these species, except *S. hastatum*, are well known from the western Atlantic Ocean, and are thought to have crossed from there to the eastern Atlantic Ocean. *Sargocentron hastatum*, thus, is an exception. Although the genus *Sargocentron* has its greatest diversity in the Indo-Pacific Ocean (Randall 1998), *S. hastatum* is a species restricted to the eastern Atlantic and does not occur south of Angola.

Luiz-Júnior et al. (2004) reported on the occurrence of four eastern Atlantic fishes that have migrated from east to west, *Acanthurus monroviae, Aulostomus strigosus, Epinephelus margina-*

rus, and *Parablennius pilicornis*, or 3.7% of the 106 reef-associated amphi-Atlantic fishes. The addition of *S. hastatum* raises this number to five, or 4.7%.

ACKNOWLEDGMENTS.— We thank the following divers for assistance in field work: Any Wilk, Les Wilk, Scott Chandler, Patti Chandler, and Bill Tewes. We also thank Dive St. Vincent and Scuba San Andres for assistance in the surveys.

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FIGURES 1–3. *Sargocentron hastatum*, St. Vincent. Photo by Les Wilk.
FIGURE 4. *Sargocentron hastatum*, San Andres. Photo by Keri Wilk.

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ADDITIONS TO THE ACANTHACEAE OF ARIZONA.— Two species of Acanthaceae are reported from Arizona for the first time. Both *Carlowrightia texana* and *Ruellia parryi* have been collected recently in Chihuahuan desertscrub in the southeastern portion of the state (Cochise County). Illustrations of both species and identification keys for all species of *Carlowrightia* and *Ruellia* in Arizona are provided. Fifteen species of Acanthaceae are now recognized as native to the state.

***Carlowrightia texana* Henr. & T.F. Daniel, Madroño 26:27. 1979.**

ARIZONA: **Cochise Co.**: San Pedro Riparian National Conservation Area, Upper San Pedro River floodplain near old Tombstone River gauge, ca. 2 mi N of Hwy. 82, 31°45.244′N, 110°12.87′W, 6 Sep 2002, *E. Makings 1299* (ASU).

This represents the first collection of the species in Arizona, where it is infrequent on a rocky granite substrate at 1153 meters elevation in Chihuahuan desertscrub dominated by *Acacia greggii*, *Larrea tridentata*, *Rhus microphylla*, *Prosopis velutina*, *Flourensia cernua*, *Talinum angustissimum*, and *Acourtia wrightii*. The locality in western Cochise County represents the westernmost known occurrence of the species. A detailed description *C. texana* was provided by Daniel (1983); illustrations of the species are available in the protologue (Henrickson and Daniel 1979) and in Powell (1988); its pollen was figured in Daniel (2004); and Figure 1 shows some of the major morphological attributes of this taxon. It can be distinguished from other species of *Carlowrightia* in Arizona by the following key:

1. Shrubs to 2 m tall; corolla purplish, lower-central lobe not keel-like or enclosing stamens; anthers yellow; leaves sessile to subsessile, lamina linear, 4–35 times longer than wide, midvein only evident; head of capsule subglobose to partially flattened. . . . . *C. linearifolia*
1. Perennial herbs, usually less than 1 m tall; corolla white (often with colored markings or veins), lower-central lobe keel-like, at least partially enclosing stamens; anthers maroon (turning blackish); leaves generally petiolate, lamina lanceolate to ovate to cordate to elliptic, 1–3.7 (–5.3) times longer than wide, several orders of venation evident; head of capsule distinctly flattened laterally.
    2. Corolla 8–18 mm long, upper lip with a yellow "eye" surrounded by maroon markings; bracteoles subulate to triangular, 0.3–1.3 mm wide; seed margin dentate; Sonoran desertscrub . . . . *C. arizonica*
    2. Corolla 5.5–7 mm long, upper lip lacking a yellow "eye," veins of all lobes usually maroon; bracteoles foliaceous, usually petiolate, ovate to elliptic-lanceolate, 0.7–5 mm wide; seed margin entire; Chihuahuan desertscrub . . . . *C. texana*

Carlowrightia texana occurs in Chihuahuan desertscrub, mesquite woodlands, and oak-juniper woodlands in the southern United States (Arizona, New Mexico, Texas) and northern Mexico (Chihuahua, Coahuila, Nuevo León, San Luis Potosí, Sonora). Plants have been collected at elevations from 25 to 1700 meters. Throughout its range, *C. texana* flowers from March until November. Arizona plants flowered in September (possibly in response to summer monsoonal rainfall). In Arizona the species is undoubtedly rare, but it likely occurs elsewhere among the isolated regions of Chihuahuan desertscrub in the southeastern portion of the state. The nearest known occurrence of *C. texana* to that reported here is about 75 km to the southeast in northeastern Sonora, Mexico, from which state the species was recently (Daniel 2004) reported for the first time.

***Ruellia parryi* A. Gray, Syn. Fl. N. Amer. 2(1):326. 1878.**

ARIZONA: **Cochise Co**.: S-facing slopes of big limestone hill, N of Guadalupe Canyon Road, 31°21′01″N, 109°06′54″W, 1372 m, 8 Apr 2001, *M. Chamberland 1900* (ARIZ).

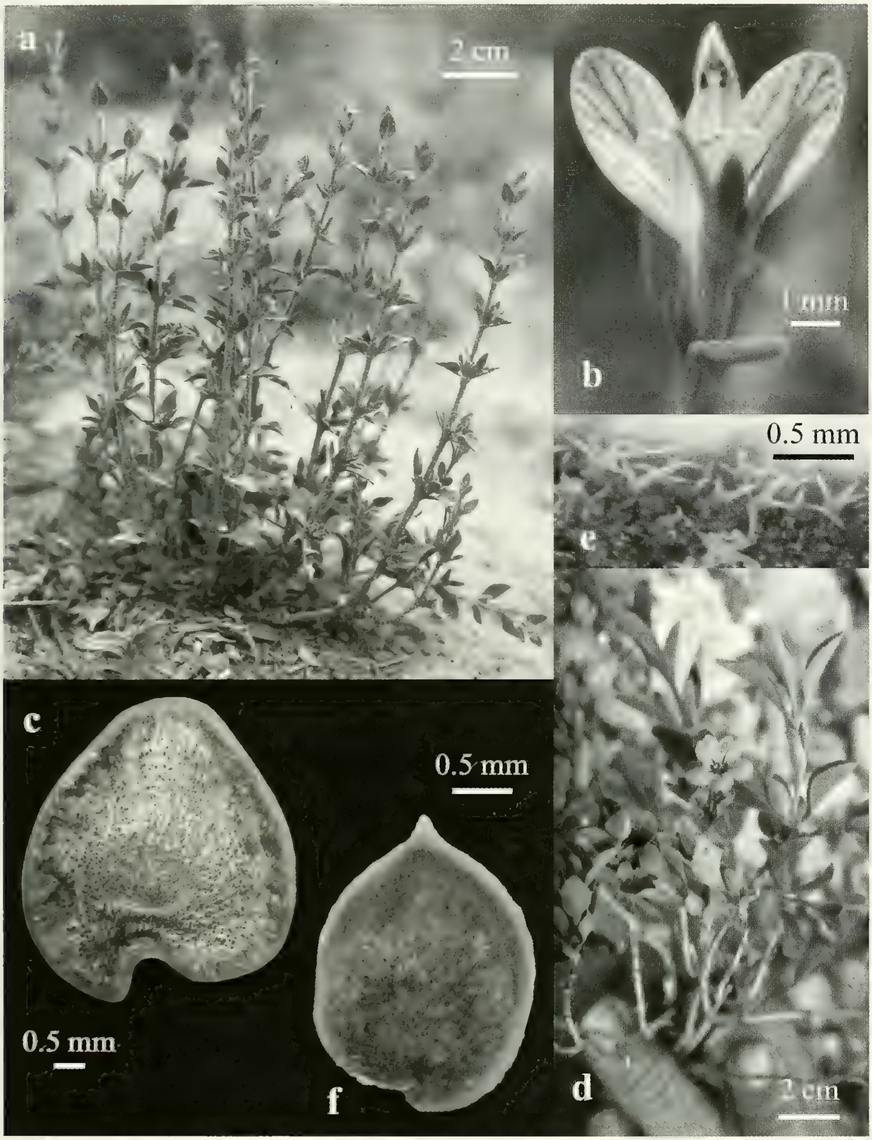

FIGURE 1. *Carlowrightia texana* (a–c) and *Ruellia parryi* (d–f). a. Habit (*Daniel 100*). b. Flower from above (*Daniel 108*). c. Seed (*McVaugh 8204*). d. Habit with flower (*Daniel 581*). e Branched trichomes from leaf surface (*Reina G. et al. 2003-957*). f. Seed (*Breedlove & Mahoney 71916*).

Ruellia parryi (Fig. 1) is reported here for the first time from Arizona, where it occurs in southeastern Cochise County. Daniel (1984, 2004) provided descriptions of *R. parryi*; its pollen was figured in Daniel (2004); and illustrations of the species can be found in Vines (1960), Wasshausen (1966), and Powell (1988). The species occurs in the southwestern United States (Arizona, New Mexico, western Texas) and northern Mexico (Chihuahua, Coahuila, Durango, Nuevo León, Sonora, Zacatecas). Plants occur on limestone in Chihuahuan desertscrub and juniper chaparral at elevations from 500 to 1950 meters. Throughout its geographic range flowering takes place from March through October. In Arizona, flowering plants were collected in April from a region of

Chihuahuan desertscrub (associated species: *Fouquieria splendens*, *Atriplex canescens*, *Quercus pungens*, *Rhus microphylla*, *Tecoma stans*, *Salvia parryi*). *Ruellia parryi* was also recently collected in northeastern Sonora for the first time (Daniel 2004), about 45 km southwest of its occurrence in Arizona. The two species of *Ruellia* known from Arizona can be distinguished as follows:

1. Herbs from woody caudex; leaves 20–170 mm long, 10–90 mm wide, attenuate at base, surfaces lacking any branched or stellate trichomes; inflorescence of (1–) 3– many-flowered dichasia borne on peduncles up to 85 mm long from axils of leaves or distal bracts; calyx (9–) 11–25 mm long, anterior lobes not fused for half or more of their length; corolla lobes 10–12 mm long; capsule 12–22 mm long, glandular pubescent; seeds 3–4 m long. . . . . *R. nudiflora*
1. Subshrubs; leaves 9–35 mm long, 3–15 mm wide, acute at base, surfaces with at least some trichomes branched or stellate; inflorescence of 1 (–3)-flowered dichasia borne on peduncles 0.5–6 mm long from leaf axils; calyx 6–11 mm long, anterior lobes fused for half or more of their length; corolla lobes 5–10 mm long; capsule 10–13 mm long, eglandular; seeds 2.5–3 mm long. . . . . *R. parryi*

Fifteen species of Acanthaceae are now known to occur in Arizona: *Anisacanthus thurberi*, *Carlowrightia arizonica*, *C. linearifolia*, *C. texana*, *Dicliptera resupinata*, *Dyschoriste decumbens*, *Elytraria imbricata*, *Henrya insularis*, *Justicia californica*, *J. candicans*, *J. longii*, *J. sonorae*, *Ruellia nudiflora*, *R. parryi*, and *Tetramerium nervosum*. The distributions of all of these species in the state are either concentrated in or restricted to the southern counties. Among counties in the state, Cochise County in southeastern Arizona has the most species of Acanthaceae (12). This county also possesses nearly all of the Chihuahuan desertscrub in the state. The recent collections of both *Carlowrightia texana* and *Ruellia parryi* in southeastern Arizona and northeastern Sonora (Daniel 2004) suggest that additional botanical exploration of the isolated regions of Chihuahuan desertscrub in these states is warranted. *Stenandrium barbatum* is another species of Acanthaceae that might be expected to occur in southeastern Arizona and/or northeastern Sonora based on its known occurrence in western portions of the Chihuahuan Desert in New Mexico and Chihuahua (Daniel 1985).

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First Report of an Eastern United States Species of Blood-Feeding Leech, *Placobdella parasitica* (Euhirudinea, Glossiphoniidae), in California.— *Placobdella parasitica* (Say, 1824) is an opportunistic blood-feeding leech on turtles. It has been reported from 22 species and subspecies of turtles (Moser 1995; Watermolen 1996) and 4 species of amphibians (Meyer and Moore 1954; Waffle 1963; Watermolen 1998). Any turtle species occurring in North America is considered a potential host.

Placobdella parasitica is abundant and widely distributed throughout the north-central and eastern United States, and southern Canada to Alberta (Sawyer 1972; Klemm 1982, 1985). It is most abundant in the Great Lakes region, where it reaches great numbers (e.g., 768 on one host turtle) (Sawyer 1972; Klemm 1982, 1985; Brooks *et al.* 1990). *Placobdella parasitica* is less known in the western United States.

Materials and methods.— *Placobdella parasitica* specimens (n=4) were collected on *Trachemys scripta elegans* (Red-Eared Slider) in Mission Valley, San Diego River (San Diego County, California) on 24 July, 2003. Additionally, two free-living specimens of *P. parasitica* were collected at Birch Lake, Camp Mather (Tuolumne County, California) on 4 May, 2004. Leech specimens were deposited in the Invertebrate Collections of the National Museum of Natural History, Smithsonian Institution (USNM 1026199) and the California Academy of Sciences (CASIZ 171366).

Results and discussion.— This is the first record of *P. parasitica* from the state of California. To date, no published records of species of the genus *Placobdella* have been reported from California (Sawyer 1972; Klemm 1982, 1985). Holland (1991, 1994) mentioned that leeches attached to approximately 7–10% of the population of *Actinemys marmorata* (Western Pond Turtle) in northern California and central Oregon, but referred to them as presumably *Placobdella*. These specimens could possibly have been *P. parasitica*, *P. ornata* or *P. papillifera*.

Except for two reports (Arizona and Nevada), *P. parasitica* has not been reported from west of the Rocky Mountains. The likely source of the geographic voucher of *P. parasitica* from Nevada (USNM 33987) was re-examined and has been re-identified as *P. ornata*. The voucher record of *P. parasitica* from Arizona is unknown. It is possible that *P. parasitica* may have been accidentally introduced to California with the introduction of exotic eastern and central United States turtles. *Placobdella parasitica* will likely be found in more localities in the western United States upon further collection.

Acknowledgments.— We thank the National Wildlife Health Center (USGS; Madison, Wisconsin) for collection of this species in Southern California, Dr. Dan Holland for permission to cite reports and Dr. T'Shaka Toure (USGS, Irvine, California).

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Diatoms
Taxonomy and Ecology: A Marriage of Necessity

Proceedings of a Workshop
23-27 October 2002, Kulice, Poland

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Taxonomy and Ecology: A Marriage of Necessity

Proceedings of a Workshop

23–27 October 2002, Kulice, Poland

Preface

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The workshop, "Diatom Ecology and Taxonomy: A Marriage of Necessity," was convened by J.P. Kociolek and A. Witkowski, from 23–27 October 2002 at the University of Szczecin's Conference Center in Kulice, Poland. The workshop was sponsored by the California Academy of Sciences (San Francisco), University of Szczecin (Poland), Alexander von Humboldt Foundation (Germany) and Carl von Ossietzky University (Oldenburg, Germany). A total of 48 participants from Albania, Belgium, Belarus, Croatia, Denmark, Germany, Hungary, Ireland, Macedonia, Poland, Russia, Spain, Sweden, Ukraine, United Kingdom and USA were in attendance.

A number of invited speakers raised issues related to the workshop's title, with regard to fossil and recent diatoms, and freshwater, estuarine and marine habitats. Viewpoints of those focused primarily on taxonomy and ecology were presented. The plenary presentations provided the springboard for lengthy facilitated discussions. The areas of overlap and separation were discussed, and topics that might promote synergy for the two disciplines explored. The papers comprising this volume represent most of the invited speakers at the workshop. The workshop could serve as a model for future discussions by diatomists across scientific disciplines.

The organization of and ongoing support for the Workshop by faculty, staff, and students of the University of Szczecin was above reproach. Their efforts assured our workshop's ultimate success, and the attendees were both aware of and greatly appreciated the hard work that went into dealing with the workshop's many practical and impractical elements.

PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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Taxonomy and Ecology: Further Considerations

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In this overview, points of the initial publication by Kociolek and Stoermer are reviewed and expanded upon, noting the gulf between the disciplines of taxonomy and ecology and the modest ways the two areas currently intersect. Some research areas for synergy are suggested. Previously published data on diatom community structure are assessed in terms of decreasing taxonomic resolution. The varying levels of taxonomic refinement are compared to the original data, and argue for the finest degree of taxonomic resolution. The final session of the workshop is summarized related to the desirability and implementation of on-line taxonomic resources, especially floras.

The publication of our paper on the need for a marriage of diatom taxonomy and ecology (Kociolek and Stoermer 2001) prompted a wide range of comments and responses directed to us, some constructive, some not, and was one of the most requested either of us have ever published. It also prompted the gathering/workshop, which generated the series of papers included herein. The workshop was developed to foster dialogue on the general topic of describing and promoting ways for taxonomists and ecologists to collaborate. Despite some initial cultural hurdles, by the end of the workshop participation by the entire group was open, honest and constructive.

The present report has three objectives: First, it reviews, amplifies and (hopefully) clarifies some of the points made in the earlier paper related to integrating taxonomic and ecological studies. Second, an example is based on previously published data showing the relationship (and dependency) on ecology and relative to fine- and coarse-grained taxonomy. Lastly, one of the areas of extensive discussion that coalesced the opinions of many in the final workshop session is summarized and discussed; namely the potential and desirability of flexible, on-line taxonomic products, particularly floras.

TAXONOMY AND ECOLOGY-MORE DIFFERENCES THAN SIMILARITIES

Tradition is one of the greatest barriers separating the disciplines of Ecology and Taxonomy. The number of strictly taxonomic (versus morphological/ultrastructural) papers in the diatom literature is relatively modest, compared to the number of papers with ecology as a focal point. And the breadth of places for publications of ecological papers far exceeds the relatively smaller number of publication venues for taxonomic works. Taxonomic works rarely contain any specific ecological data-cursory summaries are usually the most offered. When included, ecological data have rarely been used to substantially forward our knowledge about the taxonomy of specific entities. Many ecological studies use taxonomy as a means to an end, but the species lists (usually containing many errors in names and authorities) usually suggest a continuation of previous approaches (and errors) rather than any serious analysis of taxonomic results (though many more diatoms are being seen by ecologists than taxonomists). Finer-grained taxonomy and the current state of flux in freshwater diatom nomenclature appear to offer difficult hurdles for ecologists. The formal structures of our discipline help to perpetuate the gulf between taxonomists and ecologists. At meetings of the international society, oral presentations are arranged to separate presentations by ecologists and taxonomists; the two groups usually meet as they pass by each other going into/out of their respective sessions.

The divide between taxonomy and ecology is reflected not only in the outright absence of taxonomists in the area of ecology, but in the approaches the two groups have to taxonomy. Although, of course, there are exceptions to the stereotypes/generalizations I offer here, I would suggest that the goal of most taxonomists is what I call "correct taxonomy," that is trying to understand the morphological variability through the ontogeny of the cell and cell cycle (Kociolek and Williams 1986), what the circumscribed taxon should be called in the context of other taxa. Assignment of the taxon under study with in the Linnaean hierarchy not only offers an information storage-retrieval system (so that other data, including ecological data) can be compared and used in a wide range of studies, including comparative autecology, comparisons across space and time, alien species), but also predictive value so the hierarchy system should express the phylogenetic/evolutionary position of the taxon (Kociolek 1998). These typical taxonomic studies are usually organized and presented in stylized formats and with jargon, which appear arcane to ecologists. The back-and-forth that can result from such studies suggest more uncertainty than certainty (recall the numerous exchanges related to the proposal of the genus *Naviculadicta* — e.g., Moser et al. 1995, Kociolek 1996). The result of these debates is a wait-and-see stance from ecologists using the taxonomy, such that the impact of much of the primary literature is delayed unnecessarily. Even when the fervor of discussion has died down, and an approach has more or less been settled upon, some have found it difficult to embrace the consensus (e.g., Camburn and Charles 2000).

To achieve their research agenda, ecologists, on the other hand, focus attention on "consistent" taxonomy, making sure that the entities they encounter in the light microscope can be reliably applied to their respective group, hopefully representing some "real" biological entity. Ecologists face the challenge to avoid "shoe-horning" specimens into already-established taxon names, and to ensure their "consistent" grouping have some biological reality.

Another way taxonomists and ecologists are separated relates to their search for places to conduct their research programs. Ecologists, for the most part, seem to be attracted to systems that have been in some way impacted, usually by the activities of human beings. A driver towards these systems and their related questions may be funding, as governments (locally, regionally, nationally and internationally) seek understanding to possible impacts and remediation required. Taxonomists tend to seek out non-impacted situations to explore and conduct their research programs. It is usually these places that support native and undescribed taxa (e.g., Moser et al. 1995, 1998; Metzeltin and Lange-Bertalot 1998), and it has been suggested that an understanding of the biogeography of freshwater diatoms has been clouded by the impacts of the human species on the distribution of species (Kociolek and Spaulding 2000). Due to human disturbance, taxonomists are less likely to encounter species that might bear on the questions they pose. Thus, an issue so basic as where we work helps to divide taxonomists and most ecologists. It should be noted, however, that as ecologists seek to understand "pristine" or "unimpacted" situations, and the structure of communities found in those types of habitats, partnering with taxonomists in the investigation of those systems would be a wonderful setting for the marriage of taxonomy and ecology.

A common concern of those using diatoms to estimate water quality is the (in)ability to identify every individual encountered in their slides/counts. Many times the specimens are rare, or in cases of taxa where the entire population has nearly synchronized division, thus encountering many individuals, but who occupy a narrow range of variation. It is well documented that two or more distinct taxa may overlap morphologically, especially at the small end of the size range (Stoermer et al. 1986; Theriot and Ladewski 1986; Geitler 1932). Thus, although it may be impossible for the practicising ecologist to undertake studies to understand the full range of variation in a taxon (thus providing insights into the identity of the taxon), it must also be realized that closely related species share many similarities (hence the close evolutionary relationship), and thus it might be difficult to separate/identify isolated individuals. An analogy might be the difficulty to identify deciduous trees to species when leaves are off the tree, but easier when leaves and flowers are out.

Thus, whereas the current state of ecological and taxonomic research is of two nearly independent fields, their interrelationships are at best utilitarian, with any dependency in terms of relationships driven by taxonomists supporting ecologists with flora (rare, actually) or serving as "hired gun" identifiers of individual or groups of species.

We believe that this separation of disciplines does not have a long, sustainable future. Integration of the two disciplines is a goal worth pursuing, with the payoffs of a more rigorous, robust enterprise (more students, more positions, research impacts and more funding) that approaches answers to questions posed by ecologists and taxonomists. Areas that are and should integrate these approaches include paleolimnology-done successfully, evolutionary ecology (especially of ecologically pristine areas), conservation biology, co-evolution, and biogeography.

TAXONOMIC RESOLUTION AND ITS IMPACTS ON ECOLOGICAL INTERPRETATIONS

The interplay between taxonomy and ecology perhaps finds no closer relationship, the marriage is not more intimate, than the use of diatoms in the assessment of ecological conditions. A myriad of approaches has evolved since the early ideas of Kolkwitz and Marsson (1908) to apply diatoms to understanding freshwater ecology in particular, especially focused on human impacts (pollution). Excellent overviews of these appoaches can be found in Patrick and Roberts (1979), Cholnoky (1968) and Stoermer and Smol (2001).

In quantitative approaches, early workers suggested robust analyses (robust in the sense of statistics/mathematical models) required enumeration of thousands (in some cases tens of thousands) of valves to achieve reliable results (e.g., Patrick et al. 1954; Hohn 1961; Hohn and Hellerman 1963; Patrick 1968). Since the days of these extensive identification and enumeration methods, efforts were made to save time in the analysis of samples and to essentially reduce/minimize cost (because many of these studies were by now in the U.S. being funded by government agencies) but derive "correct" assessments of water conditions. This has led to a variety of approaches where counts are reduced to a certain number of valves (e.g., Stevenson and Pan 2001; 300–600/sample seems to be settled upon without too much debate) or until no new taxa have been encountered (e.g., Charles et al. 2002; assuming richness plays some role in the analysis/understanding of water quality).

Although the effort has focused on reducing the number of valves to count (yet still achieving a correct assessment), few studies have looked at ways to reduce taxonomic resolution and still achieve a "correct" understanding of water quality. In other words, does all the "fuss" made by taxonomists to identify and separate taxa at the level of species, variety and form (and this is being done with renewed vigor-e.g. Lange-Bertalot and Metzeltin 1996; Reichardt 1999 as good examples) contribute in a substantitive way to our understanding of water quality?

In the era when scientists were exploring myriads of ways to apply diatoms to water quality studies, complete data sets were often published (e.g., Hohn and Hellerman 1963; Patrick 1968; Patrick and Roberts 1979), as opposed to the summary statistics and data plots seen in most "modern" analyses.

To explore whether taxonomic resolution, i.e. coarse or fine-grained taxonomy, mattered in the interpretation of ecological data, we selected data sets published by Patrick (1968) on Darby Creek, Pennsylvania (USA). For each data set, we calculated species richness and Shannon-Wiener diversity, for three conditions, including the data set as presented (with identifications made by Patrick and finest taxonomic resolution presented in the paper at that time (what we have termed “All”) and two levels of reduced taxonomic resolution. In one case, we subsumed all subspecific epithets into the species (“Species”) and then all species and subspecific epithets subsumed into genera (“Genus”). The richness and diversity calculations were then ranked for each of the 8 stations based on the three different levels of taxonomic resolution. We then made the assumption that the complete or “All” dataset, with the finest level of taxonomic resolution most closely representing the relative ecological conditions of the eight samples. We then compared these relative relationships with those derived from approaches with more coarse-grained taxonomies, to see how well they might serve as proxies for the finest-level of taxonomic resolution. We should note here that the finest-grained taxonomy applied in 1968 probably does not represent the finer distinctions made today.

Table 1. Comparison of Richness and Shannon-Weiner Diversity including all taxa.

Sample	*Richness*	*Diversity*
Sample 1		
ALL	105	4.6555
SPECIES	88	4.3523
GENUS	22	2.6942
Sample 2		
ALL	104	4.6967
SPECIES	88	4.4337
GENUS	21	2.7002
Sample 3		
ALL	103	4.9641
SPECIES	87	4.6687
GENUS	20	2.8527
Sample 4		
ALL	111	4.6429
SPECIES	95	4.366
GENUS	23	2.5449
Sample 5		
ALL	108	4.8087
SPECIES	94	4.4895
GENUS	21	2.776
Sample 6		
ALL	101	4.8705
SPECIES	85	4.5502
GENUS	21	2.747
Sample 7		
ALL	107	4.7037
SPECIES	92	4.3687
GENUS	19	2.6464
Sample 8		
ALL	112	4.517
SPECIES	98	4.2581
GENUS	23	2.4761

In Table 1 are listed the richness and diversity measures for the eight samples provided in Patrick (1968) for “All,” “Species” and “Genus.” The eight samples are then ranked from most to least rich, and from most to least diverse in Table 2. The richness and diversity measures are provided for pennate taxa only in Table 3. Ranking of the pennate taxa measures is provided in Table 4.

The data suggest that the samples were relatively rich, in the data including pennate and centric taxa, with total taxa numbers ranging from 101 to 112 in the All samples, 84-98 taxa in the Species samples and 19–23 taxa in the Genus samples. Diversity ranged from 4.5170 to 4.9641 in All samples 4.2581 to 4.6687 in Species samples and 2.4761 to 2.8527 in the Genus samples. In the rankings, sample 8 was the richest in all calculations, whereas sample 6 (All, Species) and sample 7 (Genus) were poorest in terms of taxa. Interestingly, in terms of diversity, sample 3 was most diverse in each of the three sample calculations, whereas sample 8 (the richest in terms of number of taxa) was the least diverse in all three calculations. Assuming the All samples best approximated the “true” condition, Species rankings of richness matched exactly the All calculations, whereas Genus matched only 50% of the rankings. For diversi-

Table 2. Ranking of samples by All, Species only and Genus only for Richness and Shannon-Weiner Diversity with all taxa included. “#shared” shows the number of rankings that are in agreement with All taxa.

Richness All	*Richness Species*	*Richness Genus*	*Diversity All*	*Diversity Species*	*Diversity Genus*
8	8	8	3	3	3
4	4	4	6	6	5
5	5	1	5	5	6
7	7	5	7	2	2
1	1	6	2	7	1
2	2	2	1	1	7
3	3	3	4	4	4
6	6	7	8	8	8
#shared with ALL		4 out of 8		6 out of 8	3 out of 8

ty, Species matched 75% of the rankings of ALL, but Genus matched All in less than 40% of the rankings.

Table 3. Comparison of Richness and Shannon-Weiner Diversity including pennate taxa only.

Sample	*Richness*	*Diversity*
Sample 1		
ALL	94	4.3976
SPECIES	79	4.0794
GENUS	19	2.2934
Sample 2		
ALL	95	4.4671
SPECIES	80	4.1681
GENUS	18	2.2619
Sample 3		
ALL	95	4.7224
SPECIES	79	4.389
GENUS	17	2.4439
Sample 4		
ALL	102	4.3962
SPECIES	86	4.0926
GENUS	20	2.1704
Sample 5		
ALL	100	4.6403
SPECIES	86	4.2801
GENUS	18	2.4285
Sample 6		
ALL	93	4.6821
SPECIES	78	4.3588
GENUS	18	2.578
Sample 7		
ALL	99	4.4825
SPECIES	83	4.0871
GENUS	16	2.2709
Sample 8		
ALL	102	4.262
SPECIES	88	3.9695
GENUS	20	2.0455

Table 4. Ranking of samples by All, Species only and Genus only for Richness and Shannon-Weiner Diversity with pennate taxa only included. "#shared" shows the number of rankings that are in agreement with All taxa.

Richness All	*Richness Species*	*Richness Genus*	*Diversity All*	*Diversity Species*	*Diversity Genus*
8	8	8	3	3	6
4	4	4	6	6	3
5	5	1	5	5	5
7	7	2	7	2	1
2	2	5	2	4	7
3	1	6	1	7	2
1	3	3	4	1	4
6	6	7	8	8	8
#shared with ALL	6 out of 8	2 out of 8		4 out of 8	3 out of 8

In data including pennate taxa only, richness ranged from 93–102 taxa in All, 79–88 in Species and 16–20 in Genus. Diversity ranged from 4.2620 to 4.7224 in ALL, from 3.9695 to 4.3890 in Species and from 2.0455 to 2.4439 in Genus. In the rankings, data for pennates only mirrored the total taxon scores, while sample 8 being the most rich, and sample 6 being least rich in All and Species and sample 7 least rich in the Genus calculation. Likewise, sample 3 was the most diverse and sample 8 (the most species rich) was least diverse. Order of ranking of samples in terms of richness, 6 of the 8 rankings of Species were the same as All, whereas only 2 of 8 were the same between Genus and All. Order of ranking of samples in terms of diversity, as in pennate and centric taxa, showed less correspondence between Species and All (4 out of 8) and Genus and All (3 out of 8).

These data seem to suggest that even modest changes in taxonomic resolution can lead to large changes in the relative ranking of samples (up to 50% difference). In other words, reduced taxonomic resolution does not provide accurate prediction of relative rankings of water condition. The surprising result of an inverse relationship between species richness and diversity suggest even the most common measures of water quality analysis may require further critical evaluation. Further analysis is needed, with robust statistical power, on the impacts of reduced taxonomic resolution on predicting the relative rankings of water conditions.

Creating Modern Taxonomic Tools for a Large, International User Community

The workshop discussed at length ways in which taxonomic information can best be conveyed to the broad community of diatomists, serving both taxonomists and ecologists (and others as well). Praise was evident for projects like the Süsswasserflora (Krammer and Lange-Bertalot 1986–1991), with its great taxonomic and geographic breadth, detailed taxonomic information, and incredible photo documentation. A second project also hailed by the workshop participants, though more restricted in scope, was the series on diatoms from the Baltic Sea (Snoeijs and co-workers, 1993–1998). The project succinctly brings together illustrations with listings of important literatures and helpful comments into a common, useful format. It also represents a collaboration of scientists from different labs, countries and perspectives.

Shortcomings of traditional floras include the lack of tying images or distributions explicitly to specimens in publicly accessible collections, uncertainty or lack of studies documenting synonymies, lack of detailed geographic summaries, the static nature of data and the high cost of the published volumes.

Given the limited number of formally trained taxonomists and systematists worldwide (Kociolek and Stoermer 2001) and the increased possibilities for interaction and collaboration afforded by the internet, many workshop participants saw the opportunities and benefits of developing an on-line flora. This concept has been discussed in part by Kociolek (accepted). Such a flora could also be linked to/integrated into other information systems that are already in place or in development that offer templates for achieving additional goals (offering the ability for users to provide comments and feedback, allowing the flora to create dialogue and be a dynamic entity for several possible communities; see one example dealing with the freshwater diatoms of south Florida (and the system in place at Academy of Natural Sscience, Phildelphia [ANSP] as current examples). The call for on-line tools such as floras was recently presented in *Science* (Wheeler et al. 2004).

Information that can be an integral part of an on-line flora include name (linked to databases on nomenclature), description, important references (linked to on-line literature databases), verified distributions (linked to collection/herbarium databases), reported distributions (linked to literature databases), images (linked to image databases), types (linked to collection databases) and the person(s) responsible for the entry information. There is currently being developed enough information infrastructure available on-line such that an on-line flora is possible. It is time for members of the diatom community to work towards producing this much-needed tool—a tool that would serve both taxonomists and ecologists.

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A Review of Diversification Trends in Diatom Research with Special Reference to Taxonomy and Environmental Applications Using Examples from Lake Baikal and Elsewhere

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The study of diatoms has diversified strongly since its beginnings in the 18th century. Early work focused upon collecting material for taxonomic analysis but by the mid 19th century a strong global perspective had already developed. In the 20th century, use of diatoms in biostratigraphy, environmental change and ecology and in biogeography proliferated as did work on diatom ultra structures, life cycles, and systematics. Most recently, systematics and molecular genetics have sought to reveal diatom genealogy and to refine taxonomy. Similarly, diatoms are used increasingly as time-space indicators of water quality and there is renewed interest in global diversity patterns. Taxonomy underpins these applications but changing concepts can either diminish or enhance the value of diatoms to the environmental sciences. Some ways in which taxonomic analysis of diatom assemblages can benefit environmental research are discussed with reference to material from Lake Baikal and elsewhere.

Because of their intricate siliceous cell walls and their global distribution in aquatic and terrestrial environments, diatom microalgae have attracted the interest of naturalists and researchers alike since the 18th century. Nevertheless, it was mainly during the 20th century that the value of these organisms in ecological and, due to their resistant skeleton, in palaeo-environmental research became fully recognised. In recent decades, the major role of diatoms in global primary productivity and the carbon cycle has been demonstrated (e.g., Round et al. 1990). At the same time, concern has increased about global biodiversity and the survival of species. Although microorganisms, diatoms are relevant to these issues. They are major contributors to global primary productivity and are abundant in all the earth's major aquatic ecosystems, from the oceans, through wetlands to the alpine lakes. These ecosystems are all perceived as being threatened indirectly or directly by human activities, and time-space changes in the distribution of diatom taxa can provide valuable evidence about the nature and pace of global environmental change.

There are several ways in which diatoms are particularly relevant to global change and biodiversity issues. They are species diverse and, because of their well known ecological tolerances, they can indicate the nature of environmental change (climate, pollution, and habitat loss, for example). Diatom-environment data sets are now widely available whereby diatom assemblages can be used to predict nutrients, pH and salinity in freshwaters (see Stoermer and Smol 1999; Battarbee et al. 2001). However, with renewed interest in the 'ecological quality' of habitats, species monitoring and species comparisons using diatoms (especially in combination with other organismal groups) play an important role in the ecological assessment of water quality types (e.g., Coste et al. 1991). Consequently, diatoms are included within the recently introduced Water Framework Directive (WFD, see Foster et al. 2001) for the ecological management of European fresh and transitional waters (e.g., Kelly 2002). Long-term monitoring programmes are particularly useful for detecting trends in inter-annual species change, in relation to acidify for example (Monteith and Evans 2000).

A special characteristic of the diatoms is their ability to form rich sedimentary archives, and this has been exploited in a variety of palaeo-environmental applications from marine biostratigraphy to recent pollution. Sedimentary diatoms are also becoming increasingly useful in conservation policy and management of water quality, particularly those issues focused upon in the WFD, where identification of reference conditions for impacted water bodies is required. Sedimentary diatoms, as well as other sub-fossil organism in dated sediment cores, can provide excellent ecological records of pre-impact conditions and can be used to identify modern reference lakes (Flower et al. 1997). The particular value of palaeolimnological techniques is the provision for providing a variety of reference data where information from long-term monitoring and other sources are absent (Smol 2002).

Application of diatom analysis to environmental issues rests fundamentally on adequate, precise and harmonized taxonomic conventions and techniques. The recognition of morphotaxa in the environment and the unambiguous attribution of ecological optima and tolerances are the essence of diatom-based palaeolimnological reconstruction and of diatom ecology. Even without attribution of these optima, the recognition of taxa remains of fundamental importance to other aspects of diatom research such as biogeography and systematics. Recent developments in diatom taxonomy regarding biogeographical limits for some diatom taxa and the re-definition of many taxa according to new taxon concepts (Mann 1999) have considerable implications for diatom based environmental studies. In the short-term, there is inevitable confusion concerning the new concepts (Stoermer 2001) but, if a more precise, comprehensive and appropriate taxonomic system arises, both diatom diversity appraisal and diatom ecology/palaeoecology will benefit. This paper provides an overview of the diversification of diatom research and examines some issues, applications and implications of recent taxonomic revisions for assessing diatom diversity.

DIVERSIFICATION TRENDS IN DIATOM RESEARCH

Diatoms are readily observable in the light microscope and their occurrence was well known by the late 18th century (see Round et al. 1990), but it was not until the 19th century that awareness of the large diversity of micro-organisms developed as microscopical techniques improved. In the past 150 years or so, diatom research has diversified into several major fields ranging from ecology and micropalaeontology to systematics and molecular genetics. Although these diversification trends are indicated broadly in Figure 1, some of the perhaps less known recent applications are omitted (e.g., toxicology and archaeology, see Stoermer and Smol 1999).

EARLY TAXONOMY.— The pioneering work of Ehrenberg, Greville and others during the early part of the 19th century (see Fig. 1) established diatoms as an important biological group and several classical works followed (e.g., Ehrenberg 1854). These works not only focused on describing species and erecting a taxonomic system for diatoms but the authors also were often very interested in the provenance of diatom taxa. Ehrenberg, for example, corresponded extensively with Charles Darwin seeking diatomaceous material from exotic locations. He was also aware of the significance of the indicator value of marine and freshwater taxa in samples. Darwin sent numerous diverse samples including atmospheric 'dust' collected during the voyage of the *Beagle* (Darwin 1839) and the facial paint used by the indigenous people of Tierra del Fuego (see Burkhardt and

Smith 1987). A little later Cleve reported widely on diatoms from disparate global locations (e.g., Cleve 1878, 1894/5). Hence, even at this early stage of diatom research, there was much interest in the geographic distribution of taxa. The early emphasis was mainly on obtaining material for describing new taxa, and it was not until later in the 20th century that diatoms and biogeography began to receive systematic attention (see below). The first diatom catalogues appeared in the late 19th century (Habirshaw 1877; Schuett 1896), and more specific accounts of historical diatom studies are available elsewhere (see Patrick 1982).

Biostratigraphy.— The significance of diatoms in stratigraphic sequences was recognised in the latter part of the 19th century (e.g., Gregory 1854; Kitton 1870). This work developed into diatom micropalaeontology through the studies of Hanna (1927), Calvert (1929), Jouse (1939) and others on terrestrial deposits. In the first part of the 20th century, marine diatom biostratigraphy was mainly restricted to terrestrial deposits, but with the development of deep sea sediment coring technology, palaeoceanography and diatom analysis rapidly expanded, firstly in the Pacific Ocean (Jousé 1960; Burckle 1972; Sancetta 1979; Barron and Baldauf (1995). The international Deep Sea Drilling Project and then the Ocean Drilling Programme opened up the world's oceans to palaeoceanography and diatom biostratigraphic analyses of marine sediment cores. Such analyses have enabled chrono-biostratigraphies to be established and permitted the major taxon groups to be arranged into an evolutionary series according to geological time (e.g., Strelnikova 1990). Freshwater diatom biostratigraphy also expanded and Bradbury (e.g., 1986) began examining continental scale freshwater diatom deposits in exposures and in cores. In the 1990s, deep coring of Lake Baikal (the international Baikal Drilling Programme, BDP) was begun and has recovered an essentially continuous sedimentary diatom record for the past 8 million years (BDP-98 Members 2001).

Ecology.— The 19th century workers (e.g., Gregory 1854; Smith 1856; and Kitton 1870) can also be considered as the progenitors of diatom ecology through their observations and subjective inferences about environmental preferences of diatom taxa. The value of diatoms as ecological indicators of water quality became clearer during the 20th century as the central role of water chemistry in influencing diatom taxa abundances in lakes and rivers was recognised. Firstly, the value of diatom taxa for indicating trophic gradients was established (Kolkwitz and Marson 1908), then for salinity (Kolbe 1928) and pH (Hustedt 1937–39). Environmental applications followed with diatoms being used to monitor river water quality (e.g., Patrick et al. 1954). From the 1970s, multivariate methods were developed to quantify relationships among diatom taxa and environmental variables (e.g., Birks et al. 1990). Temperature was identified in the 1900s as an important descriptor of diatom abundances, but this was later discounted (see Patrick and Reimer 1966). Temperature has attracted renewed interest (e.g., Pienitz et al. 1995), but its value as a common predictor for diatom taxa remains questionable. The tight relationships of diatom taxa with their environment nevertheless makes these organisms highly suitable for 'ecological' monitoring of water quality (e.g., Kelly 2002) and of recovery responses following partial mitigation of water acidification (Monteith and Evans 2000). Irrespective of water quality relationships, diatom floristics alone can contribute to integrated biodiversity assessment of aquatic habitats (Flower 2001).

Palaeoecology and palaeolimnology.— Nipkow (1920), working in Lake Zurich, probably initiated the environmental reconstruction approach using sedimentary diatoms. The work of Deevey (1942) and Pennington (1943) then demonstrated the value of diatoms in sediment cores for palaeolimology. With the advent of precise sediment dating, diatoms became powerful tools for reconstructing recent limnological change (e.g., Battarbee 1978). However, it was multivariate analysis of contemporary diatom-water quality data sets that made palaeolimnological reconstructions quantitative and numerically sound (e.g., Birks et al. 1990, Battarbee et al. 2001, Smol 2002). Robust models are now available for reconstructing a variety of environmental changes, including pH (Birks et al. 1990), salinity (Fritz et al. 1991) and nutrients (Bennion 1994). More recent developments include the use of oxygen isotopes in diatom silica to infer lake level changes (Barker et al. 2001) and of diatoms to indicate lake enrichment by fish (Finney et al. 2000). On longer timescales, changes in freshwater diatom species down long cores have enabled palaeoclimate inferences to be deciphered for several millions of years. For northern California, Bradbury et al. (1991) described climate driven floristic changes over the past 3 million years whereas the diatom record in Lake Baikal sediments now extends palaeoclimate information for more than 5 million years (Khursevich et al. 2001).

Life-cycles and evolution.— Diatom life-cycles interested Victorian naturalists such as GHK Thwaites and W. Smith and, in Germany, L. Rabenhorst; they described several types of reproduction strategies and spore formation (e.g., Smith 1856). Specific interest in life cycles and reproduction was energised by MacDonald (1869) and Pfitzer (1869) following their observations on division and cell size change. Cell division continued to receive much attention in the 20th century, especially from the cytological perspective (e.g., Geitler 1927; von Stosch 1958). Much about morphogenisis of the silica cell wall was understood by the 1980s (Volcani 1978). Towards the end of the 20th century, the significance of life cycle strategies and of resting stages for ecology was being emphasised (e.g., Jewson 1992). Understanding more about the detail of diatom sexuality has enabled the recognition of within species 'demes' that are reproductively isolated and sympatric (see Mann 1984, 1999). The significance of the species unit in evolution is currently under debate (*ibid.*).

Taxonomy and systematics.— In the first part of the 20th century, taxonomic research increased as Hustedt (1909) began his remarkable half century of diatom publications. Floras specific to more exotic locations also increased and included such regions as South America and Siberia (Frenguelli 1923, Skvortzow 1937). As the number of diatom taxa proliferated and nomenclatural changes ensued, a recording system for diatom names and synonyms became necessary. Comprehensive catalogues, first by Mills (1933–35) and later by VanLandingham (1967–79) and Fourtanier and Kociolek (1999), followed. Major new freshwater diatom floras, which relied mainly on photographs rather than on drawings, began to appear in the 1980s, largely due to the work of Krammer and Lange-Bertalot (e.g., 1986). Interestingly, this period (the last two decades of the 20th century) and the 1840s were the two most prolific for naming new diatom genera (Fourtainer and Kociolek 1999). The advent of electron microscopy (EM) made fine resolution of diatom ultra structures possible (e.g., Helmcke and Krieger 1951, 1953–77) and led the way to the recent taxonomic revisions and the descriptions of new taxa with more structural details. These improvements also enabled ideas about diatom systematics to advance (Simonsen 1971) and, using Hennig's ideas about cladistic analysis of shared derived characters, taxa were arranged into clades and depicted on cladograms to indicate genealogy (Williams 1985). Advances in molecular biology and in particular the polymerized chain reaction (PCR) for amplifying genetic base sequences, became available by the late 1980s. This permitted the analysis of genetic material, rather than of morphological characters, to used to infer systematic relationships within the diatoms (Bhattacharya et al.1992), leading to new ideas about diatom phylogeny.

New taxon concepts.— With the rapid developments in ultra structure, molecular genetics and reproduction, it is unsurprising that taxon concepts began to change. The diatom species concept can be based on several views (see Theriot 1992, Mann 1999), but, suffice to say here, studies using living and fossil taxa will necessarily always be at least partly based on morphological evidence. Concepts about non-species level taxa also began to change since the 1970s (e.g., Ross and Sims 1973, Lange-Bertalot and Simonsen 1978, Williams 1985, Round et al. 1990). The trend to describe new genera has expanded especially for biraphid taxa. The recent literature contains an array of these new genera, but it is littered with invalid diagnoses, conflicting designations and idiosyncrasies associated with particular authors. Molecular genetics offers a way of establishing relationships amongst taxa and to some extent validating morphotaxa (Medlin 1997). Gene sequencing work on diatoms has helped in the validation of *Aulacoseira* taxa (*cf.* Edgar and Theriot 2002), but it is unlikely that the technique can be applied to all the controversial morphotaxa in the foreseeable future.

REGIONAL FLORAS AND BIOGEOGRAPHY.— The proliferation of new names, especially in the past decade, has come at a time of renewed interest in diatom biogeography and biodiversity and in diatoms in remote areas and on islands. Whilst providing further evidence for widespread distributions of some taxa, the incidence of discontinuous distributions and endemism is becoming more widely appreciated. However, taxa with regionally restricted distributions were well known in the 19th century (see Cleve 1895/6). Endemism is a special case of restricted geographical distribution, and its high incidence in ancient Lake Baikal was recognised early in the 20th century (Dorogostaisky 1904; Skvortzow and Meyer 1928). Baikalian, Siberian (Palaearctic), relict and other endemic elements were then recognised in Baikal's benthic diatom flora. Also notable for regional endemism are the recent floras of the Patagonian region (Rumrich et al. 2000) and especially of the island of New Caledonia (Moser et al.1998). As long ago as Smith (1856), the widespread distribution of many diatom taxa as compared with higher plants was recognized, and because many diatom taxa are undoubtedly cosmopolitan, this view has persisted (Lund 2002). However, a minority of diatom taxa do appear to have restricted regional distributions, the significance of which in systematics and biogeography is now being evaluated (Williams 1995; Kociolek and Spaulding 2000).

The diversification of diatom research indicated in Figure 1 suggests that the main lines of development are diverging through time. This impression is only partly justified because current interests in diatom biogeography, biodiversity, ecology and palaeoecology are interrelated. Furthermore, morphotaxonomy provides the essential foundation for these linked lines of research. Hence, there is a necessity to improve ways in which taxonomic convention is achieved and disseminated to all investigators, researching or otherwise. Diatom diversity in time and in space has and will make major contributions to both environmental science and to evolutionary studies. One current challenge is to provide a firm validated taxonomic framework for achieving these aims.

TAXONOMIC OBJECTIVES, PROTOCOLS AND INFORMATION DISSEMINATION

The science of taxonomy is the search for natural order; or is it? According to S.J. Gould, quoted in Håkansson (2002), taxonomy is about genealogy and the search for natural order, but the *International Code of Botanical Nomenclature* (ICBN, Greuter et al. 2001) states that the role of taxonomy is simply to supply a means of referring to a taxon and indicating its rank. The binomial system, developed by Linnaeus and upon which the ICBN is founded, was conceived as an aide memoir for individual taxa and this usage persists, despite other suggested systems (*cf.* Forey 2002). The binomial names and the higher taxonomic levels can usefully indicate something about phylogeny and taxon group affinities, but it is the role of systematics to elucidate biological relationships using homologous characters or genetic markers (Kitching et al. 1998).

In much applied diatom research, the relationships amongst taxa are usually of less importance than the relationships of taxa (usually species level or below) with environmental variables. Nevertheless, typification and the unambiguous designation of diatom taxa remains of fundamental importance in both systematics and environmental applications. Use of diatoms in time-space diversity studies is increasing and requires taxonomic consistency not only for attributional reasons

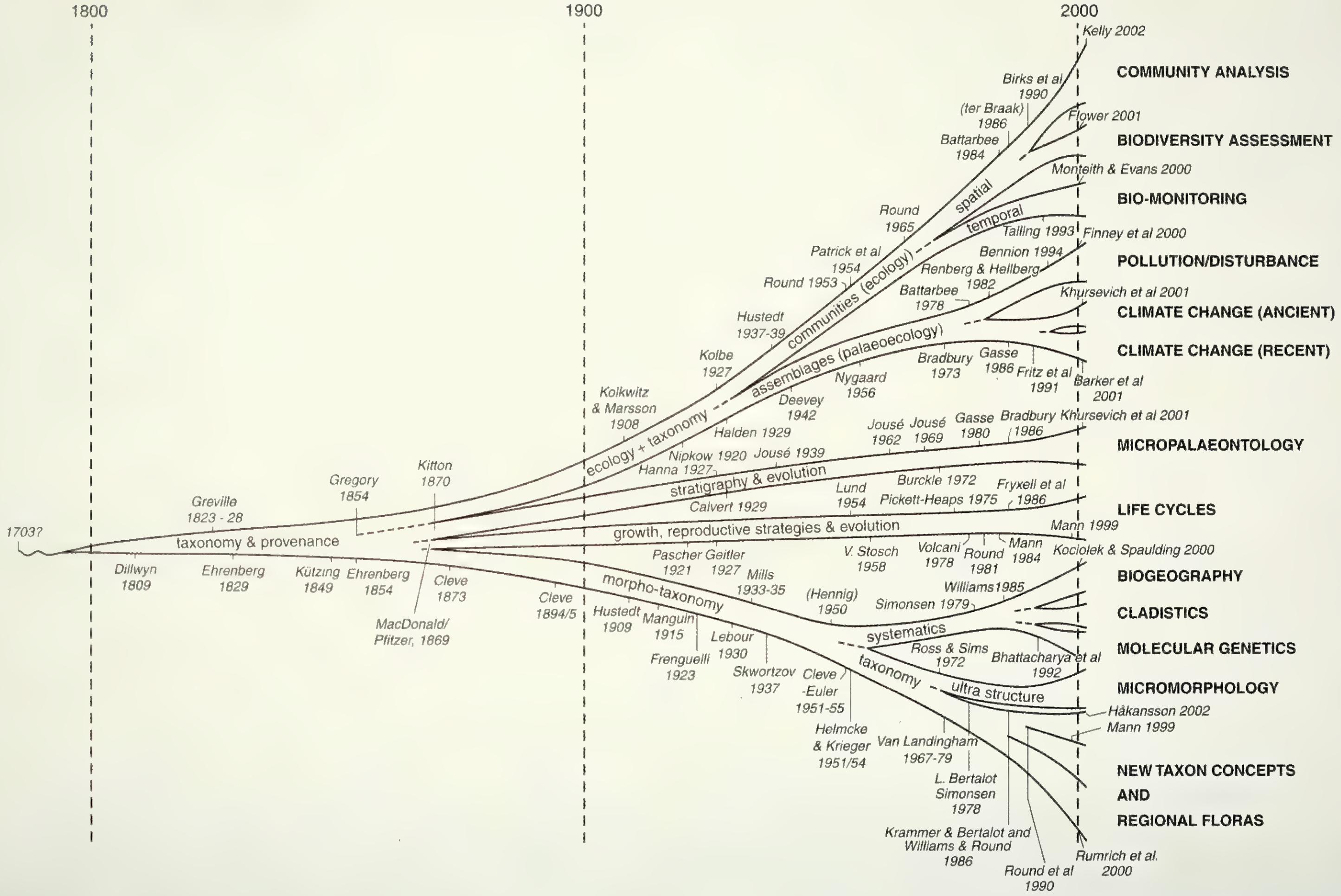

FIGURE 1. A summary diagram indicating trends in the diversification of diatom research during the past two centuries. Note that, i. several important and relevant but non-diatom references are indicated in parenthesis, ii. that the ~2000 AD array of diatom research areas is not exhaustive (see Stoermer and Smol 1999) and that the diagram does not indicate adequately the degree of interactions and facilitation between intra-subject areas.

but also for inter-flora comparisons. It is therefore wise to consider ways in which diatom taxonomy can be made more user-friendly, less 'messy' (Mann 1999) and less ambiguous to promote consistency at both local and international levels.

When a new diatom taxon is described, either at the variety (Flower 1989), species (Skvortzow 1937) or genus (Vyverman et al. 1998) level, typification should be relatively straight forward, assuming the author(s) have carefully checked the literature and relevant type material and obey the conventions (see Greuter et al. 2000). Formal typification is, therefore, regulated. In reality, however, the system is far from straight forward, and difficulties are often amplified when original investigations of particular taxa are translated into identification floras. There is currently a lack of coherence in diatom taxonomy that obstructs consistent and accurate species identifications. This is especially important for routine diatom counting within research consortia where light microscopy is principally used. Taxonomic inconsistencies amongst authors can obfuscate studies of both regional flora comparisons and species distribution patterns. There are several specific ways in which dis-harmonies can arise and these include:

1. The tendency to combine some taxa into rather broad species groups (e.g., Lange-Bertalot and Simonsen 1978) was reversed in the 1980s as many of the traditional species were subdivided into new genera (Williams and Round 1986; Round et al. 1990). This has led to conflicts in the literature (e.g., Kociolek 1998) and creating new genera by re-designation is currently on going (e.g., Round and Maidana 2001). New genera of course have merit where they better reflect different morphological groups but the ICBN definition of taxonomy suggests that some of the genus splitting effort may be questionable because whatever legitimate binomial is used the taxon characteristics are still amenable to systematic analysis.
2. The recognition of sympatric taxa based mainly on sexually incompatible subgroups or demes (*cf.* Mann 1999) raises the issue of describing and typifying many more diatom taxa. The tendency to subdivide conventional species taxa began earlier (e.g., Knudson 1953; Koppen 1975). Steps towards increased taxonomic resolution are generally welcomed by those using diatoms as environmental indicators because it can improve discrimination of environmental change (Flower and Battarbee 1985). However, if a system is adopted whereby reproductively incompatible demes are designated as species (Mann 1999), the great multiplication in names for within groups of (sympatric) taxa, all characteristic of the same environmental conditions, will contribute little more to understanding the role of environmental variables.
3. Increased taxonomic resolution and separating taxa by using details of ultra-structure is an important part of taxonomic research. However, when such details alone are used to discriminate taxa and especially at the generic level then difficulties for routine light microscopy can arise. Defining a taxon using single criteria, for example striae ultra structure (*cf. Kobayasiella micropunctata* [Germain] Lange-Bertalot) or separating two genera (*Cyclostephanos* and *Stephanodiscus*) using ultra structure detail of the external rimoportula (see Guerrero and Echenique 2001) is problematic and such ultra structure requirements led Camburn and Charles (2000) to abandon many taxonomic revisions in their work on the North American softwater diatom flora.
4. There is an increasing trend to use informal and/or (usually) inadequate descriptions of taxa in some floral and palaeoecological studies (e.g., Stevenson et al. 1991). Unverified book-form floras are extremely useful for opening up new areas for investigating diatom diversity (e.g., Rumrich et al. 2000) but they do not provide site-specific species inventories, and can obfuscate identifications by non-specialists. Informal designations can be a useful expedient, but lack of information can make widespread use of inadequately described taxa impossible (examples are many, such as *Frustulia* spec., *Cyclotella kuetzingiana* [agg.] which without accompanying images are of questionable value). Elsewhere, Gould (1989) used the term 'shoe-horning' to describe the tendency to fit potentially new taxa into pre-existing descriptions; undoubtedly this practise has caused difficulties in diatom identification and taxonomic comparisons especially amongst biogeographical regions (Williams 1995).
5. The existence of type specimens for all described taxa together with precisely catalogued synonymies should in a perfect world permit validation of problematic taxa. In practice, type specimen material is often inaccessible, unavailable, poorly conserved or is imprecisely identified. There are many cases where type

material in diatom herbaria is not mounted on glass cover slips (especially the older collections) so making observation difficult. For more modern material, type slides are often lodged in collections without any indication as to which is the type specimen. In mixed material this can make selection of the type subjective or at worst makes the preparation virtually useless for taxonomic validation purposes.

The practical problems of making type material more amenable are now being tackled as techniques to display and characterise individual specimens are ever improving. However, some taxon characteristics will always be questioned and the extents to which current literature conflicts can be rectified is debatable. Taxonomic research cannot, nor should it, be carried out by consensus, but focusing conflicts in the primary research literature would help reduce ambiguity for taxonomy users. Where integration of diatom distributions in time-space is needed, neither molecular nor cytoplasmology is likely to resolve current problems. Neglecting the value of morphotaxa in favour of other taxonomic tools is probably not yet a practicable option in most environmental work. Applied diatom research is growing and there is a pressing need to introduce more consensus into standard taxonomy. For example, European protocols for diatom monitoring of rivers (e.g., Kelly 2002) advocate use of particular identification floras, but this standardisation attempt is subjective. Some steps to reconcile current difficulties could include:

1. Abandon the binominal species name concept and develop a uninominal system (e.g., Ereshefsky 2001), so *inter alia* eliminating confusions caused by generic changes
2. Abandon the binomial naming system and develop an iconographic numerical coding system as is used for chrysophyte cysts (see Duff et al. 1995)
3. Continue with the current system but introduce a consensus platform into taxonomy in a way that reduces ambiguities and makes diatom iconographs and regional floras more accessible to end-users.

The latter step is in many ways preferable and would allow taxonomic research to continue its erratic individualistic course but permit progress towards *a coherent world diatom flora*. This flora, although very incomplete at first, could incorporate many existing works and be updated following decisions made through an authorised consensus forum. In reality, this practice has already been used to harmonise diatom taxonomy within several research consortia projects (Stevenson et al. 1991; Gell 1988; Camburn and Charles 2000). Internet and web site developments are beginning to make such harmonization procedures available on a wider scale. Nevertheless, local concepts and project driven agenda continue to dominate data sets. If AQC (analytical quality control) is to be achieved widely, a permanent over-arching central body or tightly co-ordinated group is needed. This would ideally result in a maintained web site database of images, descriptions and names for all known diatom taxa as well as provenance and environmental information.

Appropriate recording of taxonomic decisions and descriptions should follow ICBN protocols (Greuter et al. 2001) and type specimens must remain the 'gold standard' in diatom taxonomy. Using the virtually limitless capacity of web-based data sets, combined with ease of updating, makes their use attractive and considerable progress has already been achieved. See the following:

http://www.algaterra.org, for taxonomic baselines and original type material;
http://www.calacademy.org/research/diatoms/, for cataloging diatom names and synonymies;
http://www.ualg.pt/adiac, for diatom image identification aids;
http://www.geog.ucl.ac/ecrc/enclosed/darwin.htm, for diatom images from Lake Baikal;
http://www.geog.ucl.ac.uk/ukawmn, for monitoring diatom taxa and water chemistry;
http://www.craticula.ncl.ac.uk8000/Eddi, for images and taxa with ecological optima.

This latter site is particularly useful for applied diatom taxonomy users because it combines taxonomy, ecology and provenance data for application to diatom assemblages in sediment cores so that environmental reconstructions of water quality can be made (Battarbee et al. 2001a).

Diatoms are key organisms for monitoring natural water quality in Europe and elsewhere, but major taxonomic contradictions need to be reconciled. Taxonomy does suffer from a lack of global organisation and planning generally (Alberch 1993), yet taxonomic consistency is a key necessity in diatom research (Kociolek and Stoermer 2001), and it is difficult to envisage how this can be achieved internationally without access to a coherent reference system. If a web-based global image database were developed, this would *inter alia* help harmonise diatom taxonomy (for international monitoring programmes, biogeographic comparisons, etc.). However, any such international system must be (1) comprehensive, (2) have long-term maintenance/up-dating mechanisms, (3) incorporate consensus into taxonomic designations, (4) be of sufficient quality to supersede the use of book-based floras, (5) conservative regarding the verification and incorporation of new taxa from the primary literature, and (6) able to use type specimens where possible. Even if these conditions are met, some problems specific to web sites remain. The e-data are free of peer review (although authentication through consensus management could minimise this criticism), they require permanent specialist staff, and some institutional internet-servers can impart loss of transmitted image quality. Where on-line databases provide environmental data for particular taxa, revisions involving splitting taxa could invalidate any ecological optima. However, updating synonymy dictionaries could help maintain database integrity.

DIATOM DIVERSITY

Diatom diversity is an attempt to describe all the variability present in the group and as such includes an array of factors such as life forms, genetics and morphology. For evaluating time-space diversity aspects in diatom distributional studies, morphotaxon concepts are probably the most useful in the first instance. Despite difficulties in diatom taxonomic harmonisation (above), there are two main ways to consider the diversity of diatom morphotaxa, according to:

1. Spatial scales — these vary from local, through regional to global scales and are modified primarily by water quality, substrata and by biogeographic factors.
2. Temporal scales — these vary from diurnal and seasonal changes through inter-annual and millennial trends to evolution and species replacements over geological time (stratigraphic facies).

The role of temporal and spatial scales on the occurrence and distribution of organisms has a large general literature (e.g., Rosenzweig 1995). Aquatic organisms received rather less attention although environmental change and fish speciation is well researched (Ruber et al. 1998) and Brooks (1950) made a careful global study of endemicity in lakes. Both studies demonstrate the importance of morphotaxonomy in comparing systems but the former showed some morphology groups diverged from mDNA phylogeny. Nevertheless, morphotaxonomy remains the initial tool to investigate diversity. Lake Baikal is remarkable for both speciation and endemicity (Kozhova and Izmesteva 1998), yet the benthic diatom diversity of Baikal requires thorough re-assessment (see Mann 1999, Flower et al. 2004). This lake can be used as an example for diatom diversity studies from several aspects.

LAKE BAIKAL AND TAXON DISTRIBUTIONS.— Lake Baikal has a large endemic component in its diatom flora. Most of the planktonic diatoms are endemic as are about half of the benthic taxa (according to Skwortzov 1937). This latter estimate will almost certainly need revising upwards (Mann 1999). Initial work on common shallow-water taxa around the lake (Flower et al. 2004) has not demonstrated any major distributional relationships associated with the three main sub-basins. Hence, these diatoms provide no evidence that the Lake Baikal sub-basins were isolated in the past (*cf.* fish populations in Lake Tanganyika [Ruber et al. 1998]). However, distributions of the large conspicuous endemic taxa (mainly in the deep littoral) remain largely undescribed (Flower et al. 2004). The shallow water taxa appeared to be mainly cosmopolitan forms, but careful examination indicated that some of these too might have restricted distributions. Common *Synedra vaucheriae* (*sensu* Skvortzow) occurs in two characteristic forms in Lake Baikal. Similarly, in Lake Baikal, *Hannaea arcus* (*sensu* Skvortzow) seems to be a new species although it is not restricted to the lake (Bixby 2002).

The more conspicuous deep water benthic endemic taxa in Baikal, e.g., *Didymosphenia dentata* Dorog. are thought to be entirely restricted to the lake (Kociolek et al. 2000). A consideration of the lineage of gomphonemoid taxa suggests that this species evolved in Baikal (*ibid.*) but verification by fossil records is needed. The fossil record can offer definitive evidence about past taxon distributions and immigrations (*cf.* Bradbury 1986). Being able to draw conclusions about the origin of taxa has important bearings on interpreting modern distributions. This is why the Baikal Deep Drilling Project cores and the ~ 5 million years of sediment records are so valuable with many new species and even genera being described (Khursevich et al.2001). Although this palaeowork so far indicates *in situ* evolution of endemic planktonic taxa (*ibid.*), benthic diatoms often comprise up to ~10% of the sediment record and their stratigraphic records need evaluating. However, the Baikal record is so extensive that it may be difficult to find comparable sedimentary diatom facies elsewhere for evidencing ideas about speciation. Fossil material from the Vitim Plateau (NE of Lake Baikal) is lodged at the Baikal Museum (see Flower et al. 2004) and casual examination has indicated the presence of several current Baikal endemic taxa (*Aulacoseira baicalensis* and *Cyclotella baicalensis*), indicating wider Siberian distributions of these taxa in Pleistocene lakes. The situation regarding fossil benthic taxa is largely unknown.

Lake Baikal and diatom regionality.— Some common benthic diatom taxa in Baikal that appear to be rather different from the normal concept of the species form (e.g., *Synedra vaucheriae*) are probably restricted to the Baikal region. *Cymbella stuxbergii* and *Eunotia clevei* also occur in Baikal but have wider though still restricted distributions (Williams et al. 1999; Reid and Williams 2001). Other taxa were recognised by Skvortzow (Skvortzow and Meyer 1928; Skvortzow 1937) as having distributions restricted to Asia. However, many of the satellite lakes around Lake Baikal possess entirely different floras to that in Baikal, but there are important differences in water quality. Also, all the upland satellite lakes have only existed since the last glaciation. In Lake Bolshoie in the Khamar Daban Mountains above Lake Baikal, the surface sediment is dominated by the plankton diatom *Pliocaenicus costatus* v. *sibirica* (see Flower et al. 1998). This diatom genus is mainly known as a fossil, but the taxon is extant in a few sites in Siberia. With only a very few exceptions, the benthic diatom flora of Lake Bolshoie is otherwise very similar to oligotrophic upland lakes in the UK. The unusual distribution of this planktonic taxon seems to be linked more with a limited dispersal and biogeography rather than with special water quality preferences.

Regional issues regarding the relationships of Lake Baikal endemic diatoms with closely related taxa elsewhere can be examined using systematic analysis (*cf.* Williams 1985, 1996). This offers one way of placing Baikal's endemic flora in an evolutionary context by defining lineages. Quantitative comparisons using morphological characters possessed by both the endemics and closely related taxa offers an alternative to using the fossil record. This approach has been applied to *Stephanodiscus* in the USA (Theriot 1992) and to benthic *Tetracyclus* spp. (Williams 1996), but its application to Lake Baikal taxa is perhaps premature. Here the first priority is to provide a thorough inventory of the benthic taxa within the lake, to revise previously described taxa, and to provide an iconograph for the benthic taxa.

Lake Baikal and measuring diversity.— Assessing diatom diversity in a large lake such as Baikal presents practical as well as theoretical difficulties. Size can be tackled by systematic sampling (*cf.* Flower et al. 2004), but measuring species diversity offers a variety of challenges. Biodiversity estimation has a considerable literature and an array of methods (Hawksworth 1995; Heywood 1995). Traditionally, a range of ‘biodiversity indices’ have been applied to multi-species sample populations and much information on species:area distributions has been generated (Rosenzweig 1995). Interestingly, however, diatom taxa do not seem to show the expected number and area relationship (Allen et al.1999) probably for reasons of water quality (Flower 2001). Yet assessing diatom diversity is important and may benefit from an approach other than application of the traditional indices. Refinements for assessing diversity by taxic measures, such as the ratio of genera to species (see Hawksworth 1995), and by phylogenetic methods to reconcile species numbers with genealogical divergence (Williams 1996), are interesting concepts. However, like molecular genetics, using these techniques to address general issues of diatom occurrences and abundances in Lake Baikal and many other poorly described areas must *inter alia* await an adequate base in morphotaxonomy.

No single diversity measure can capture all aspects of ‘diversity’, and at sites such as Baikal, measures that ignore the significance of endemicity are incomplete. However, getting taxonomy to the level where Baikal’s endemic taxa can be validated in routine diatom analysis remains a major challenge (Flower et al. 2004). Identifying any with in hot spot regions of Baikal for endemic taxa is not yet feasible. Estimates of species richness are, however, relatively easy to make, if consistency in morphotaxon identifications is maintained rigorously (*ibid.*). Partitioning taxa into rare and non-rare categories is an additional measure of ecological quality for a particular site or habitat (see Gaston 1994). Most diatom samples can be characterised by a few common species and a limited number of rare taxa (van Dam 1982), and for Baikal the rare taxon category often captures some of the conspicuous endemics. For shallow water epilithon samples, taxon abundance distributions (examples in Fig. 2) were plotted for 51 stations around Lake Baikal (see Flower et al. 2004). There are considerable variations between abundances of common and less common taxa in each sample. Rather than make assumptions about these distributions (*cf.* Rosenzweig 1995), it is instructive to consider the rare taxa alone. Rare taxa can be defined in various ways (Gaston 1994):

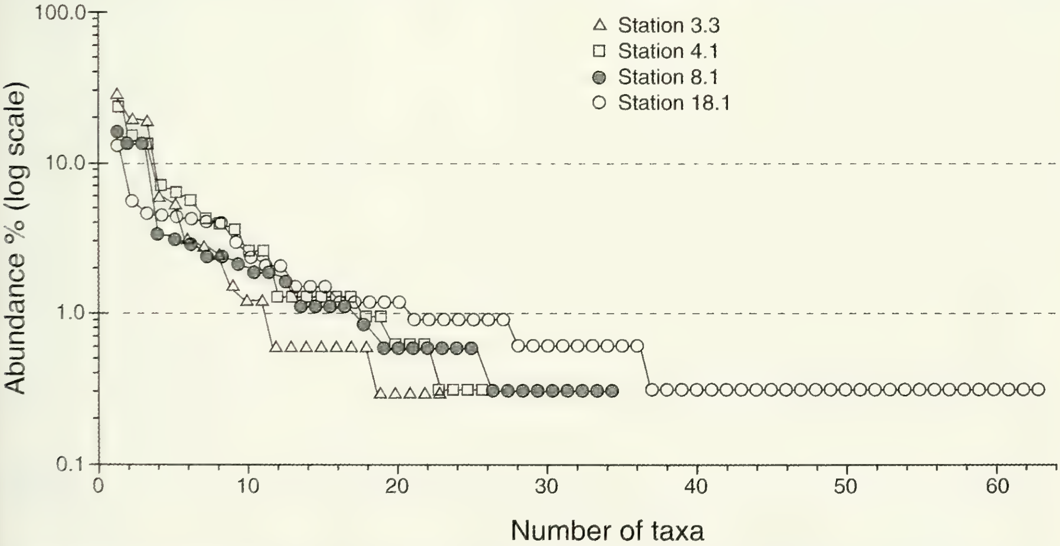

FIGURE 2. Relative abundance rank curves for diatom taxa in several shallow water epilithon samples selected from collections made from 51 sampling stations around Lake Baikal in 1997/98 (see Flower et al. 2004).

they occur at very few sites (either locally or internationally); they are always found at low abundances; or they may be perceived as rare because of identification problems. For these Baikal samples, the 'rare' taxa are those with frequencies of <1% in a fixed count of 300 valves (see Flower et al. 2004).

The rare taxon data can be used to generate a simple index that places an emphasis on the proportion of rare taxa in samples. The relationship between diatom taxa occurrences and abundances is usually log-normal (van Dam 1982), and it is implicit in the log series of species-abundance distributions that the total number of species in a sample is proportional to the number of uncommon or rare species (e.g., Pielou 1974). Nevertheless, the precise relationship between abundant and rare taxa may be of potential value in assessing the relative ecological value of a site, sub-sites or a group of sites. An index of diatom rarity is indicated below. Where n is the number of sub-samples and 1 indicates the population or region of interest, V = the total number of valves counted and z is the number of taxa present at frequency abundances of 1% or less.

A simple diatom rarity index:

$$\text{Diatom rarity index = For sample 1} \quad 1- \left(\frac{\sum_{i=1}^{n} V_i}{\sum_{i=1}^{n} V_i + \sum_{i=1}^{n} Z_i^2} \right)$$

TABLE 1. Diatom rarity index values (see text) calculated from diatom taxon abundances in shallow water epilithon samples collected from around Lake Baikal (1997/98) and summed to represent each shore zone in each of Baikal's three main basins (WSB=West shore South Basin, WMB = West shore Middle Basin, WNB= West shore North Basin, ENB = East shore North Basin, EMB = East shore Middle Basin and ESB = East shore South Basin).

Shore Zone	*WSB*	*WMB*	*WNB*	*ENB*	*EMB*	*ESB*
Station scores	0.25	0.21	0.36	0.46	0.52	0.80
	0.55	0.32	0.40	0.49	0.64	0.60
	0.52	0.18	0.25	0.29	0.66	0.55
	0.14	0.46	0.52	0.49	0.78	0.43
	0.40	0.49	0.49	0.36	0.60	0.29
	0.55	0.21	0.46	0.40	0.66	0.43
	0.43		0.43	0.43		0.49
	0.32		0.46			0.32
			0.86			0.43
Mean scores	0.39	0.31	0.47	0.43	0.64	0.48

This index should be <1 assuming rare taxa are always present and the term 'rare' is subject to the count constraints imposed during sample analysis. There is, of course, a substantial number of taxa that are so rare that they will not be captured by this modest count total. In fact, cumulative counting of one Baikal sample (34.1) indicated that only above a count total of 650 valves did the count/taxon curve begin to approach the asymptote. Nevertheless, by carefully fixing the count total, the index can be used to make within lake comparisons amongst communities (Fig. 3) and amongst regions (Table 1). Increasing the standard count size will produce more taxa per sub-sample, but when a large number of samples required for comparison, the key factor is to keep the total count size constant.

LAKE BAIKAL AND DIATOM BIOGEOGRAPHY.— The large number of endemic taxa in Lake Baikal is also of interest to ideas about ubiquity and the global distributions of micro-organisms (*cf.* Finlay and Clarke 1999). Round (1981) indicated that freshwater algal taxa were more widely distributed geographically than marine taxa but that some freshwater diatoms (*Asterionella, Stephano-discus*) were restricted by water quality. Round (1981) also noted that distinctive distributional patterns existed but that studies were very incomplete. Diatom endemicity in Baikal offers a major challenge to ideas about ubiquity. The diatom flora of Baikal is demonstrably able to resist invasions and displacement by cosmopolitan species (which generally predominate in small lakes around Baikal). The recent fossil record shows continuous domination by endemic taxa (Flower et al. 1996). Elsewhere and against conservative ideas about diatom distributions, regional diatom endemicity is well recognised, in Australasia at both genus and species level (Tyler 1996) and on some oceanic islands (Moser et al.1999).

FIGURE 3. Diatom rarity index (see text) values as histograms calculated from shallow water epilithon samples from Lake Baikal (collected in 1997/98) from around the lake (see Flower et al. 2004).

There appear to be several types of endemism in Baikal arising from recent *in situ* speciation or preservation of relict taxa (neoendemics and palaeoendemics *sensu* Cronk 1992). Forms of *Navicula lacus-baicali* (Mann 1999) are probably recent whereas some species of *Tetracyclus* (Williams et al. 2002) have a substantial geological record. In the fossil record, *Aulacoseira baicalensis* seems to post date many endemic *Stephanodiscus* and *Cyclotella* taxa (Khursevich et al. 2001). *Eunotia clevei* and *Pliocaenicus costatus* are examples of taxa that are not endemic to Lake Baikal and its environs but nevertheless display distributions that are more restricted today than in the recent geological past. In some continental areas elsewhere, the impact of past glaciations were probably of paramount importance in obliterating centres of endemism and diminishing former wider distributions of ancient taxa. It is notable that much of southern Siberia, like most of Australasia, was not directly affected by major Pleistocene ice sheets. Those lakes that have persisted through major environmental changes are more likely to have retained ancient taxa (see Brooks 1950). Conversely, palaeoendemics seem absent in the post-glacial Great Lakes of North America. The contemporary endemic taxa of Lake Baikal seems largely restricted to the Baikal region and have been unable, possibly through poor dispersal mechanisms or lack of ecological niches, to expand elsewhere.

Making floristic comparisons amongst different regions to delimit the distributions of particular taxa can demonstrate clear biogeographic patterns for some taxa (Williams 1995; Kociolek and Spaulding 2000). However, making quantitative comparisons using communities is more difficult, not least because of differing taxonomic concepts and methodologies. Nevertheless, this approach is needed to establish precise taxon based floristic distances between communities or assemblages (see Flower et al. 1997) and to explore the proportional mix of cosmopolitan and endemic or otherwise restricted taxa at a particular site or location. For an extreme and preliminary quantitative comparison of two regional floras, Correspondence Analysis (see Jongman et al. 1987) of combined data was undertaken. These data comprised, (1) 51 samples of shallow water diatom epilithon samples from around Baikal and, (2) 28 samples of epilithon and surface sediment diatoms from the Falkland Islands (R. Flower, unpublished) on the opposite side of the globe (Fig. 4). Sampled substrata were not constant but other sampling and counting variables and taxonomic concepts were consistent because both data sets were enumerated by the same analyst. The most noticeable feature of this initial and crude analysis is that the amount of floristic variation in all the Baikal samples is very much less than that displayed by the 28 individual water body samples on the Falkland Islands. Also, there were only seven taxa common to both data sets and included such cosmopolitan species as *Cocconeis placentula, Navicula cryptocephala* and *Staurosira construens*.

The major floristic differences between Baikal and the Falklands samples clearly do not offer an unequivocal test of a biogeographic hypothesis for diatom distributions. Diatom taxa are particularly good indicators of water quality and are used by palaeolimnologists essentially for this reason. We would, therefore, not

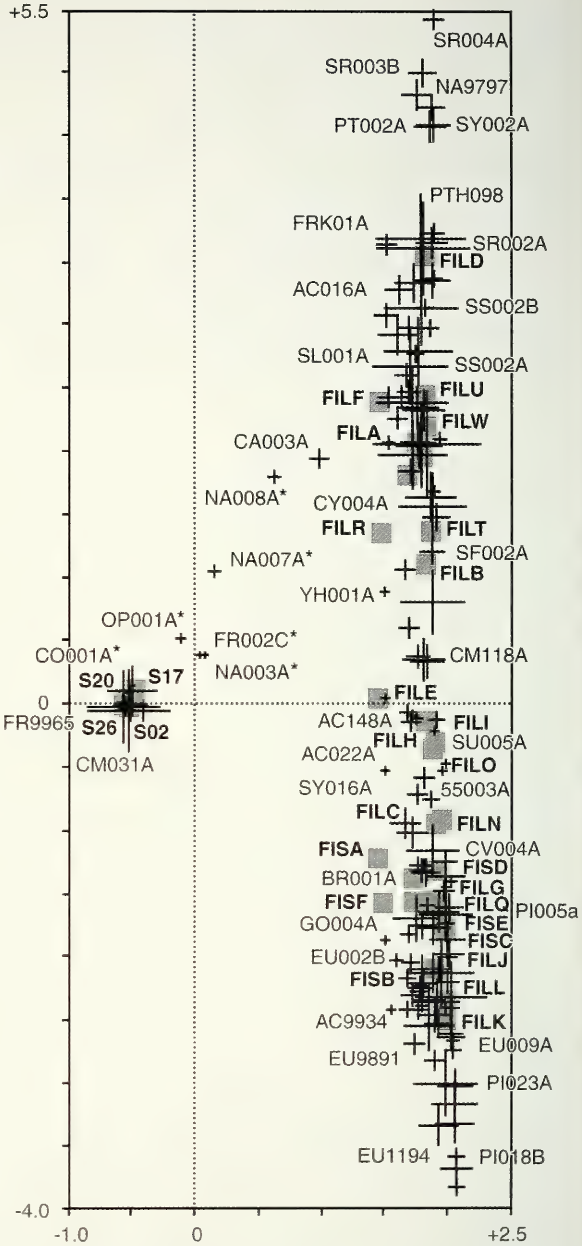

FIGURE 4. Correspondence analysis ordination of a combined data set of diatom taxa (shown as selected alpha-numeric taxon codes and crosses proportional to frequency abundances) and sites (shown as squares and coded with a bold S or FI prefix to indicate Siberian Lake Baikal or Falkland Islands sites). Note, floristic variation is relatively small for the Baikal sites and that few taxa are common to both data sets (see text).

expect ubiquity in species distributions: acidiphilous or alkaliphilous taxa do not commonly occur in calcareous or in siliceous geological regions respectively. Falkland Islands' inland waters were mainly acid. Hence ecological factors could explain most of the taxon differences in the two regions tested and very few, if any, of the Falklands Island diatoms are endemic (as on other glaciated islands, Foged 1964). On the other hand, the extremely basic rocks, unusual water quality and geological time has produced many new species in New Caledonia (Moser et al.1999). From these few observations it is likely that the incidence of diatom endemicity is affected by a variety of factors including, (1) longevity of habitat, (2) extreme environments or environmental instability (palaeoclimate or geological change), (3) proximity to centres of evolution and, perhaps, (4) the nature of the community founder species.

Evidence from numerical comparisons of inter-continental floras is scarce, but higher plant diversity (species number in disjunct genera) is higher in eastern Asia than in North America and seems mainly caused by physiographical heterogeneity in conjunction with climate change (Qian and Ricklefs 2000). Explanations of the spatial differences in diatom distributions must also involve climate, but heterogeneous geochemical conditions are probably more important locally. Causes of large scale differences in diatom distributions can be polarized into two main standpoints. One is based primarily on vicarience biogeography and the existence of regional floras arising from evolutionary events. The other is based on an assumption that taxa have global distributions that are punctuated by ecological conditions. Distributional patterns in the global diatom flora — at least for inland waters — seems to be the result of various combinations of these influences as modified by local ecology and sympatric events. However, a fuller picture of global patterns and trends in diatom diversity cannot be made until consistent floristic comparisons and time and space evaluations are undertaken for more biogeographic regions.

SOME CONCLUSIONS

Ecology, evolution, biogeography, systematics and palaeontology have drifted apart during the 20th century (Ricklefs and Schluter 1993) and a similar trend has occurred within diatom research. Recent major developments in the latter regarding species concepts, speciation, life cycles and molecular biology have all made important contributions but, for the foreseeable future, morphospecies concepts will dominate environmental studies where living and fossil taxa are used. Where concepts about diatom taxonomy and taxon designations have changed markedly, some ambiguities have arisen that give current cause for concern. Reconciling ever-finer resolution of taxa combined with nomenclatural revisions threaten to out-strip the capabilities of end-users (the ecologists, palaeoecologists). Whilst debate is necessary, the current lack of coherence in diatom taxonomy is now hindering some areas of applied diatom research, especially where light microscopy is routine. Introducing more consensus in diatom taxonomy at a level that is accessible to end users is advocated. Developing a more unified approach to accessing diatom type material and nomenclature, regional floras and ecological information through the Internet medium is one promising way of improving taxon designations and identification.

Diatom ecologists generally use the taxonomy available in published floras to identify taxa so that relationships between diatoms and measurable environmental variables can be discriminated. Diatom species distributions are not however always a predicable response to water quality and *inter alia* biogeographical factors can play an important role in the provenance of some taxa. The interplay of biogeographical and water quality factors as an influence on discontinuous distributions of diatom taxa requires the attention of both ecologists and systematic taxonomists. Any 'marriage of necessity' between ecologists and taxonomists (*sensu* Kociolek and Stoermer 2001) that would help tackle the central issue of explaining diatom species distribution patterns on time-space scales that vary from ancient to modern (e.g., Khursevich et al. 2001) and local to continental (e.g., Fig. 4) is desirable. However, disentangling the causes of these patterns will require consideration of speciation processes, dispersal mechanisms, ecological tolerances, biological interactions and of environmental change. The existing extensive and essentially morphotaxonomic diatom reference system will doubtless endure as the foundation by which research proceeds and unifying and extending this database must facilitate progress.

Despite some of the current difficulties in diatom taxonomy and its relationship with ecology, many endemic or regionally restricted diatom taxa are well defined and offer compelling evidence for the existence of biogeographic factors. They are an important aspect of global aquatic diversity assessment and maintaining global biodiversity has become paramount as anthropogenic changes proceed at unprecedented rates. Sites such as ancient Lake Baikal are hot spots for aquatic diversity and the planktonic and benthic diatom communities are largely endemic or otherwise restricted. Diversity can be measured in a variety of ways and morphotaxa concepts are usually the primary tool to investigate species time-space changes in the environment. However, where taxonomic knowledge is incomplete, concepts about species richness and rare taxa can offer a pragmatic ways of appraising the composition of diatom communities. Such measures cannot substitute for species level inventories or assess the significance of genealogical relationships within communities. Nevertheless, an optimal combination of these measures should help floristic comparisons and define community characteristics. Irrespective of taxonomic discrepancies, diatoms are increasingly important for setting baselines and references conditions and evidencing environmental change through multi-scale studies of their distributions and relationships. These are all essential parts of global biodiversity assessment in aquatic ecosystems.

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Diatom (Bacillariophyta) Flora of Albanian Coastal Wetlands Taxonomy and Ecology: A Review

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The Albanian coast still features interesting and important lagoons and other wetlands, characterised by high biodiversity. The present paper focuses on their diatom flora: taxonomy and ecology. The cheklist of hitherto identified taxa contains about 430 taxa observed in different coastal habitats, e.g., Butrinti, Karavasta, and Lezha. From the diatom structure, an evaluation of the ecological values and the trophic state of some coastal ecosystems can be made. In some of these (e.g., Butrinti), diatom and peridinophyte blooms, formed by potentially toxic species (e.g., *Pseudonitzschia seriata*, *Prorocentrum micans*, and *P. minimum*), were observed during the summer. The blooms were probably the result of the limited water exchange and were enhanced by other environmental factors (i.e., temperature, nutrients).

Studies on the ecology and taxonomy of brackish water diatoms should always be interrelated with and supported by integrated environmental programs. In the existing programs dealing with coastal wetlands, the ecological aspect is always manifestly important. However, the ecological goals cannot be satisfactorily achieved if the need for a basic taxonomic approach is neglected, which is often the case. Recently, numerous geobotanical and ecological studies of the diatom flora of lagoons from regions with different climatic conditions have been made (e.g., Miho 1994; Danielidis 1980; Witkowski 1991; Bak et al. 2001; Trobajo 2003). Similarly to other Mediterranean countries, Albania features a high diversity of species and sensitive habitats, which are rather poorly known and remain exposed to a significant impact of human activity (NEA/AKM 1999).

Biological zonation and/or the natural trophic/saprobic status of coastal lagoons can be established by studying the taxonomy and ecology of the diatom assemblages present (Miho 1994; Miho and Mitrushi 1999; Bak et al. 2001; Silvestre et al. 2002; Trobajo 2003). Such studies provide a substantial aid in exploration of biodiversity and functioning of food webs in coastal areas (Essink, 2003) and prove useful in assuring and strengthening further efforts towards their protection, restoration and sustainable use.

Publications on microscopic algae in Albania began with sporadic taxonomic surveys by foreign algologists, e.g., Forti (1902) in Shkodra Lake, Beck (1904) in Prespa Lake, Protic (1907) in brackish water habitats of Vlora, Krenner (1926) in the Drini River and Uherkovic (1963) in Shkumbini and some other rivers. Albanian studies were initiated in the 1980s. During 1987–1991, Miho (1994, 1996) surveyed the phytoplankton in Butrinti lagoon. These were expanded by research on the relationship between microalgae species composition and the trophic status of the habitats studied (e.g., Ohrid and Prespa lakes, Shkumbini and other rivers, Lezha and Vlora lagoons, glacial lakes, e.g., Miho1998a, 1998b; Miho and Mitrushi 1999; Miho and Dedej 1999; Miho and Lange-Bertalot 2001, 2003; Miho, Cake, and Carcani [in press]; Cullaj et al. 2003). Dedej (1994, 1995) provided also some preliminary data on the phytoplankton of the Durresi and Karavasta regions. Recently, Rakaj (2002), Rakaj and Kashta (1999) and Rakaj et al. (2000, 2001) have reviewed the Lake Shkodra phytoplankton. Some other publications, i.e., those by Hustedt (1945), Jurilj (1954) and Vilicic et al. (2002) are important taxonomic contributions, particularly with respect to diatoms.

The present paper reviews the diatom flora of the Albanian coastal wetlands, and is an example of how taxonomy and ecology can be mutually supportive. In addition to the floristic composition, information on the ecological and trophic status of various coastal wetlands is provided.

GENERAL BACKGROUND

Albania is a small country that extends between a high mountain range and the Adriatic Sea, bordering Montenegro and Kosovo to the north, the Republic of Macedonia to the east and Greece to the south (Fig. 1). The country features large wetland areas surrounded by evergreen hills along the Adriatic coast; in addition, almost two-thirds of the country's surface area is covered by high mountain ranges (up to 2700 m) separated by valleys. The Albanian coast is about 427 km long, 273 km along the Adriatic Sea and 154 km along the Ionian Sea (Kabo 1990–91).

The low accumulative Adriatic coast extends from the Buna/Bojana delta to Vlora Bay (Fig. 1) and is characterised by the presence of fluvial deltas, inlets and lagoons, beaches, coastal sand bars, rocky promontories, submerged caves, sandy dunes and extended inland bays. Estuaries of major rivers intersect the coast: Drini, Buna, Mati, Ishmi, Shkumbini, Semani, and Vjosa that run westwards from the country's interior (Kabo 1990–91). The rivers are major water conduits not only for Albania, but also for the whole eastern Adriatic Sea. In their eastern sections they are torrential and erosive, whereas in the Western Coastal Plain they generally form wide meandering beds.

In contrast, the Ionian coast is steep, mountainous and rocky, intersected only by a few small rivers, such as the Bistrica and Pavlla. The coast also features some small wetlands and islets. The region is characteristic in its high diversity of habitats and species. In addition, it supports active aquaculture and fisheries, while urbanisation and industrial activities are limited. Butrinti, a wetland complex, unique in its biodiversity and aquaculture, is situated in the southern part (Fig. 1).

COASTAL WETLANDS AND THEIR ECOLOGICAL VALUES

Despite reclamation for agricultural purposes during the past decades, Albania still has about 109 km^2 of coastal wetlands or lagoons. Kabo (1990–91) described the main hydrological characteristics of Albanian lagoons, and the ecology has been reviewed by Peja et al. (1996). The most important coastal wetlands are Karavasta, Narta, Lezha, and Patoku on the Adriatic, and Butrinti on the Ionian coast (Fig. 1). The lagoons extend along the coastline and are separated from the sea by rather narrow sandy spits, which continuously change in size and shape. They are generally characterised by brackish waters, being connected with the sea through one or more channels.

Generally, wetlands display a large number of biotopes with enormous diversity of aquatic flora and fauna. Moreover, they are important especially for wintering of migratory birds (more than 70 species; NEA/AKM 1999). Some of these wetlands, e.g., Narta and Lezha, are partly protected. Regarding richness in habitats, flora and fauna (especially globally threatened water birds, i.e., the Dalmatian pelican) Karavasta and Divjaka National Park area have recently been designated Ramsar sites (Ramsar 1971, convention on wetlands [see *<http://www.ramsar.org/*

profiles_albania.htm>]). Wetland areas have a very substantial economic potential for tourism, as breeding and refuge habitats for fish, and as valuable aquaculture sites. According to Peja et al. (1996), up to 6,000 kg of fish has been annually harvested during periods of high productivity.

Karavasta lagoon (surface area 43 km^2), situated between the Semani and Shkumbini deltas, is the largest of Albania. It is connected with the sea through three short channels. Divjaka forest (12 km^2) spreads out in the northwest of the lagoon (Kabo, 1990–91). It is a typically dune forest, bordered by brackish or freshwater, where pines (*Pinus halepensis* and *P. pinea*) grow up in old dunes, mixed with shrubs, grasses or reeds near lagoon shores. The lagoon system of Lezha is 10–15 km long and 3 km wide with a total area of about 22 km^2, 11.6 km^2 consisting of lagoons (Ceka, Merxhani, and Kenalla), 2 km^2 forests (Vaina and Kune) and 7 km^2 of wetlands. Their origin is related to deltaic processes of the Drini River. Narta, situated in the southern part of the Vjosa delta, covers 42 km^2 and connects with the sea via two channels. All these lagoons are shallow and fluvial in origin. Butrinti (16 km^2) is one of the most interesting lagoons of tectonic origin. Due to its relatively great depth (averaging 14 m), its water column is permanently stratified. Its bottom is characterized by anaerobic decomposition. However, during the past few decades, the lagoon has been used intensively in aquaculture of mussels (*Mytilus galloprovincialis*) (up to 2,000 to 4,500 ton gross product/year).

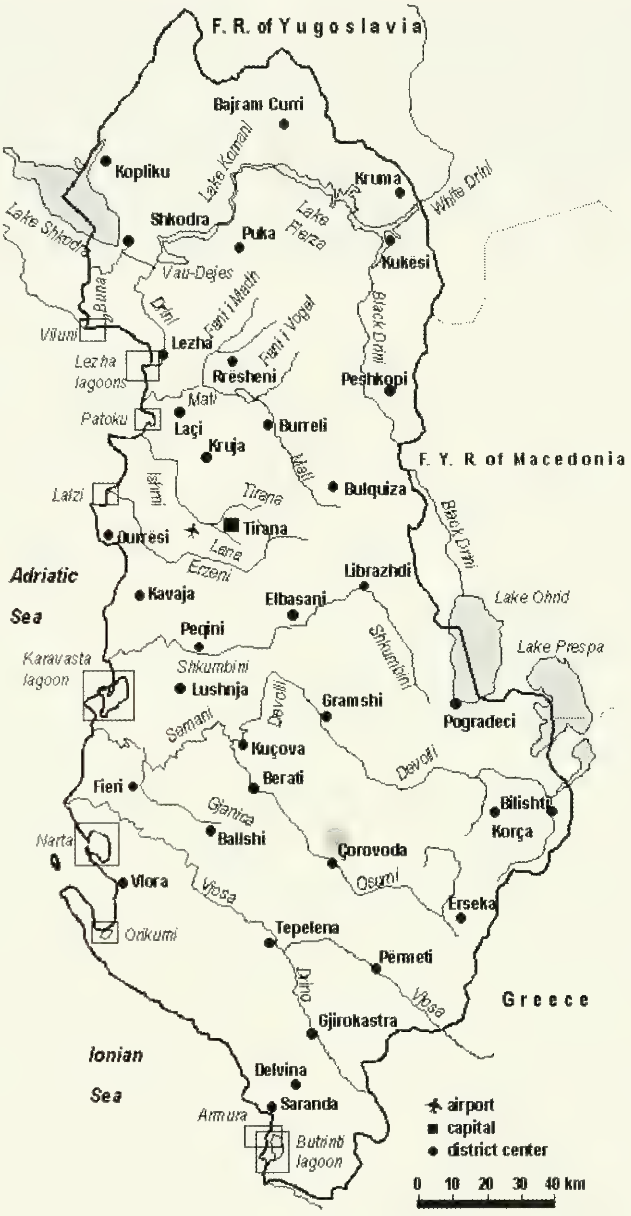

FIGURE 1: Location of Albanian coastal wetlands.

The wetlands are, however, very sensitive ecosystems that were under strong impact in the past due to the extensive agricultural reclamation and unsustainable industry. At present, the western lowland supports densely populated industrial centres, intensive agriculture and tourism.

Therefore, some riverine waters (i.e., of Ishmi, Tirana, Lana, Gjanica, etc.) are heavily loaded with urban and industrial sewage discharged directly to rivers that transport this load to the sea. Moreover, high levels of heavy metals have been found in Vlora and Durresi bays, Mati delta, etc. Petroleum industry in Fieri and Vlora also result in an adverse ecological impact on the Semani and Vjosa deltas and their related lagoons. Coastal dune forests are under pressure of touristic development. Also, the high rate of erosion caused by excessive woodcutting, overgrazing or firing in realtive shallow water basins, further increases the amount of suspended matter transported to the sea by the rivers (Cullaj et al. 2003; UNEP 2000).

DIATOMS: TAXONOMIC APPROACH

The survey of recent publications on Albanian waters, including the lakes on its borders, shows the number of diatom species to exceed 1 200. The most interesting area seems to be Lake Ohrid with about 550 species (Miho and Lange-Bertalot 2003), of which more than 100 are endemic or rarely occurring species. In their 1999–2000 study of Albanian freshwater diatom flora, Miho and Lange-Bertalot identified 900 taxa, including some whose distribution is poorly known (Miho and Lange-Bertalot 2001, 2003). Some of these (*Aneumastus albanicus*, *A. rosettae*, *A. humboltianus, Navicula pseudoppugnata, N. parahasta N. hastatula*, and *Cymbopleura albanica, C. lura* and *C. lata* var. *lura)* have recently been described as new to science in Lange-Bertalot (2001) and Krammer (2003), respectively.

Altogether, more than 430 diatom taxa were identified in the brackish water coastal wetlands, either published or presented here for the first time. Of this group, 365 taxa are pennate and 65 are centrics. More than 160 taxa were found in Butrinti and about 115 in Karavasta, representing two ecosystems with the highest number of taxa. The checklist of the species identified is given in table 1. Despite the efforts to avoid synonyms or changed names of longer established taxa, some *taxa* might be recorded here twice under different names and some identifications may not be correct. Selected taxa (13 taxa in 25 figures), either the most abundant ones or those taxonomically interesting, are illustrated in Plates I and II. The data from this compilation represent the first step to shed light on the diatom flora of this Mediterranean area, hitherto unknown. About 240 taxa have already been published, whereas about 110 were not recorded before in this area; therefore, about 80 taxa have not been observed in Albanian samples examined previously.

Vilicic et al. (2002) have already published a checklist of phytoplankton taxa in the Eastern Adriatic Sea, referring to the Croatian coast. In all, 888 taxa were reported, of which 518 were diatoms (330 pennates and 174 centrics). The data refer to naturally eutrophic areas (bays, estuaries), harbours, etc. However, only 118 taxa were also included in the Albanian checklist reported here. Probably, the difference in comparison with the Croatian checklist could be due to the fact that many of the Albanian samples were of periphyton. In addition, the various habitats differ in relation to their ecology.

Protic (1907) provided the first data on some brackish habitats from the Albanian coast (in Orikumi and Narta: Vlora region). His list included 196 species, 107 of which were diatoms. When dealing with phytoplankton of Butrinti, Miho (1994, 1996) reported 90 species, 60 of which were diatoms. This was the first ecological approach to study an important habitat, at that time intensively used for aquaculture. The diatom genus *Nitzschia* was represented by the highest number of species; however, centrics, especially *Chaetoceros* spp. and *Cyclotella* aff. *choctawhatcheeana,* were the most abundant. The difficulty in their identification was the principal taxonomic problem. As a matter of fact, more than 40 taxa in Table 1 are not fully determined. Other abundant species included *Pseudonitzschia seriata*, *Nitzschia capitellata* and *Thalassionema nitzschioides*. They were accompanied by peridinophytes, e.g., *Prorocentrum micans*, *P. minimum*, *Scrippsiella* sp., *Ceratium fusus*, *C. pulchellum*. In the three Lezha lagoons (Ceka, Merxhani, Kenalla), about 90 phytoplankton species were recorded in July 1996 (Miho and Mitrushi 1999). A relatively high diversity was observed in Merxhani where *Chaetoceros* spp., *Amphora holsatica*, *Nitzschia sigma*, *Entomoneis paludosa*, *Cerataulus turgidus*, *Melosira nummuloides*, *Grammatophora oceanica*, *Pleurosigma angulatum* and *Striatella unipunctata* were observed as abundant species. In Ceka, an algal bloom was observed, dominated by *Nitzschia reversa*, *Peridinium* spp., *Gonyaulax monacantha*, and *Prorocentrum minimum*. Kenalla, a relatively deep pond close to the shallow lagoon of Merxhani, supported large populations of the centric diatom *Chaetoceros muelleri*, associated with abundant filamentous blue-green algae, e.g., *Anabaenopsis circularis*, *Oscillatoria* sp., and a small peridinophyte *Gymnodinium* sp.

Occasional surveys were also carried out in other Albanian wetlands, i.e., Saranda, Karavasta, Narta, Patoku, Viluni and Durresi (Lalzi) (Miho 1998b). In Karavasta, 65 diatom species were identified. In this locality, again, pennates represented by the genera *Fragilaria* and *Cocconeis* prevailed. In 1992–93, more than 75 diatoms were identified in the Orikumi wetland, where pennates also dominated. In a recent assessment of different habitats of Butrinti, Armura and Saranda Harbour, spanning the period of 1998–2000, over 200 epiphytic diatoms were identified. These included 28 centric species, represented by *Cyclotella* (6 species), *Actinocyclus* (5), and *Chaetoceros* (4), as well as 178 pennates, including, e.g., *Nitzschia* (25 species), *Mastogloia* (20), *Amphora* (14) and *Navicula* (12). The most abundant taxa included *Cyclotella* cf. *choctawhatcheeana*, *Achnanthes brevipes*, *Amphora* cf. *tomiakae*, *A. coffeaeformis*, *Bacillaria paxillifer*, *Cocconeis placentula*, *C. scutellum*, *Staurosira construens*, *Mastogloia crucicula*, *Nitzschia coarctata*, *N. constricta*, *Pleurosigma formosum* and *Thalassionema nitzschioides*.

Certain species, interesting either from an ecological or taxonomical point of view, are presented below. Some of them represent the dominant organism, whereas others are poorly known.

Cyclotella aff. *choctawhatcheeana* Prasad (Plate 1: Figs. 1–9) was abundant in the phytoplankton of Butrinti (Miho 1994) where it was responsible for an autumn bloom. The species occurred as solitary cells or colonies and was present in the water column throughout the growing season. *C.* aff. *choctawhatcheeana* occurred in combination with various *Chaetoceros* species. In other Albanian lagoons (Orikumi, Karavasta) the distribution was scarce and represented by single cells only. Albanian specimens belong to the *Cyclotella caspia* group and are closely related to *C. choctawhatcheeana* Prasad; however, some characters differ from the descriptions given by Prasad (1991), Wendker (1991), and Hakansson et al. (1993). Unlike *C. choctawhatcheeana*, the Albanian specimens possess 1–3 fultoportulae in the middle; the transapical striae were radiate but finer, about 30–40/10µm, and measured 5–15 µm.

Chaetoceros spp. (Plate 1: Figs. 10–14): the species belonging to the genus *Chaetoceros* occurred abundantly in the phytoplankton of the lagoons, especially in Butrinti, Orikumi, and Merxhani. However, due to their very fine structure, it was not easy to identify the most common species. Nevertheless, as shown by Miho (1994), *Ch. wighamii* Brightwell seems to be the most abundant, characterised by very small colony-forming cells with very fine setae.

Actinocyclus cf. *subtilis* (Gregory) Ralfs (Plate 2: Fig. 2) was found in brackish and almost marine waters, e.g., Butrinti and Armura Bay (Saranda). Based on their overall morphology, our specimens resembled *A. subtilis* (Gregory) Ralfs. However, they differed from this in having a generally larger valve diameter (exceeding 68 µm) and denser areolation of the striae (more than 16 puncta/10 µm). The taxon appears to have morphologically distinct valves; according to the species description by Witkowski et al. (2000), *A. subtilis* valve diameter is smaller and the striae possess a coarser areolation (about 12/10 µm).

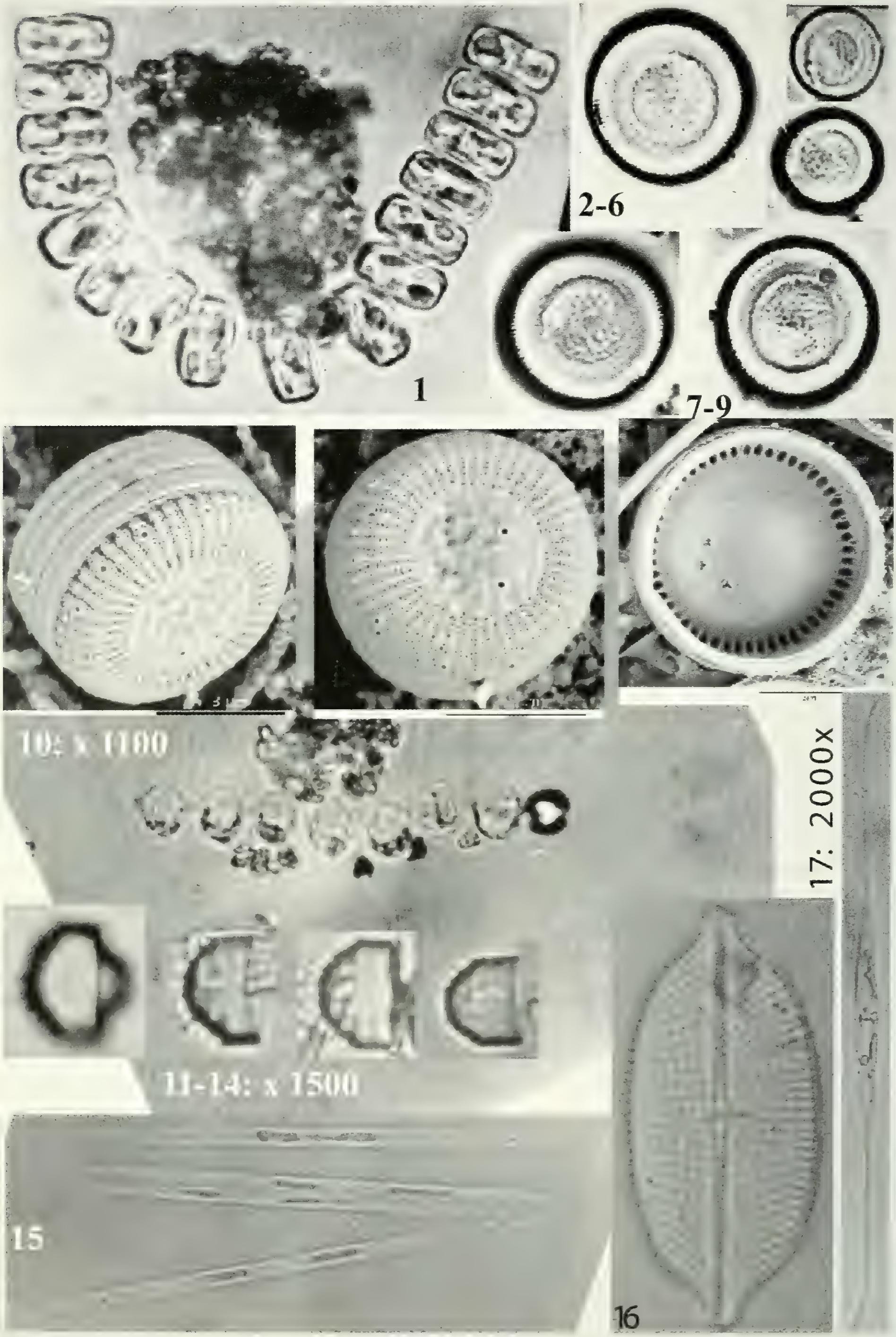

PLATE I. Figs. 1–9: *Cyclotella aff. choctawhatcheeana* Prasad; Figs. 10–14: *Chaetoceros* sp. diverse (cf. *Ch. wighamii* Brightwell): Fig. 7–9. SEM. bar = 3 µm): Fig. 15: *Pseudonitzschia seriata* Cleve: Fig. 16: *Navicula* cf. *besarensis* Giffen: Fig. 17: *Nitzschia reversa* W. Smith. (Figs. 1–6. 11–16: 1500×: Figs. 7–9: SEM. bar=3 µm: Fig. 10: 1100×: Fig. 17: 2000×.)

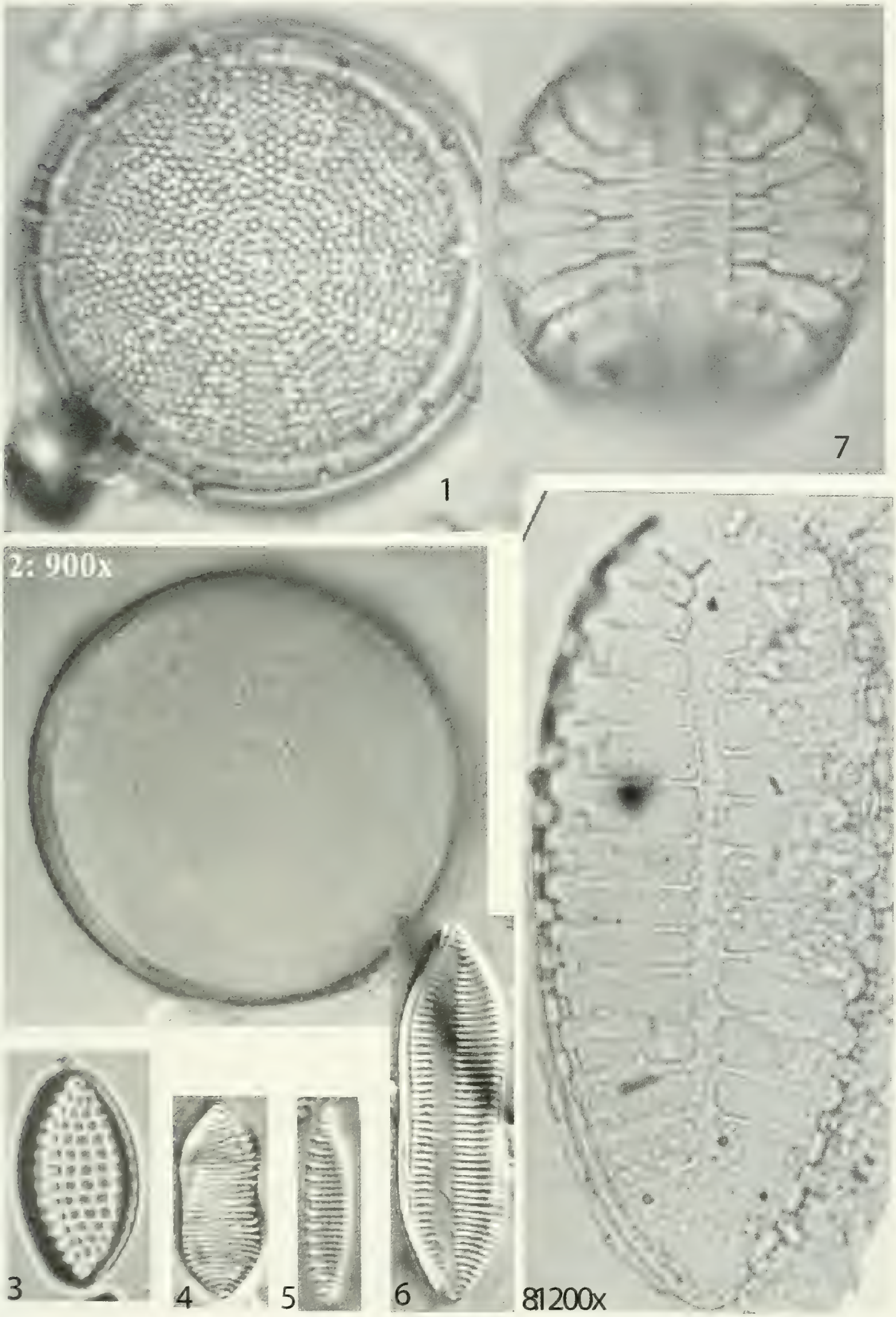

PLATE II. Fig. 1: *Actinocyclus* cf. *ochotensis* Jouse; Fig. 2: *A.* cf. *subtilis* (Gregory) Ralfs; (900x) Fig. 3: *Nitzschia granulata* Grunow; Fig. 4: *N. coarctata* Grunow; Fig. 5: *N. constricta* (Kützing) Ralfs; Fig. 6: *Campylodiscus* cf. *simulans* Gregory; Fig. 6: *Surirella* cf. *fluminensis* Grunow. (Figs. 1, 3–7: 1500×; Fig. 2: 900×; Fig. 8: 1200×.)

Campylodiscus cf. *simulans* Gregory (Plate 2: Fig. 7) was found in Butrinti and Saranda Bay. The morphology seems to be intermediate between that of *C. simulans* Gregory (Schmidt's Atlas: Tafel 17, Figs. 12–14) and *C. thuretii* var. *baldjikiana* Grunow (Plate 51, Figs. 16–21).

Surirella cf. *fluminensis* Grunow (Plate 2: Fig. 8) is a poorly known species. The morphology appears to be similar to that of the specimen drawn in Schmidt's Atlas (Plate 5: Fig. 6). Specimens were 44–62 µm long and 23–27 µm broad with 8 ribs/100 µm. The axial area was relatively narrow. This organisms were frequent in Karavasta and scarce in other Albanian lagoons.

Nitzschia reversa W. Smith was found to form blooms in Ceka lagoon (Lezha) (Plate 1: Fig. 17). It is characterised by sigmoid valve shape (35–95 µm long and 2.5–3.5 µm broad) and a very fine striation (not resolvable in LM). It was smaller and finer than the specimens from the type population characterized in Witkowski et al. (2000) or Proshkina-Lavrenko (1955).

Pseudonitzschia seriata Cleve (Plate 1: Fig. 15) was very abundant in Butrinti lagoon. During late spring and summer of 1987 it was observed to form a bloom (Miho 1994).

DIATOMS: ECOLOGICAL APPROACH

Guelorget and Perthuisot (1984) have proposed a biological zonation system for lagoons, based on their 'confinement', a hydrological parameter linked mainly to exchange/renewal of the water. It can be based on benthic communities, where each community characterizes one of the six defined zones. Therefore, each zone has its own specific richness, density, biomass, productivity (including phytoplankton), etc. Hence, based on the composition of the microalgae, such zonation could be drawn up, and as a consequence a diagnosis of the biological and economic potential of a lagoon could even be made. Here, some preliminary insights into biological zones that prevail in Albanian lagoons are presented, based on the algal assemblages.

Butrinti ranks among typical meromictic water bodies; therefore, optimum conditions for phytobenthos are to be found in some borderline locations, dominated by *Enteromorpha prolifera* (Miho 1994, 1996). The remaining part of the bottom is affected by anaerobic conditions, characterized by high rates of organic matter sedimentation and decomposition. Thus, the primary production is virtually due to the phytoplankton of the upper layers (5–7 m depth), which was dominated by one or two species of centric diatoms (often accounting for more than 90% of the primary producers). The seasonal pattern involved a very pronounced peak in spring (up to 44,000 cells/ml in March 1991) and a smaller one in the autumn. A phytoplankton decline, accompanied by a relative increase in peridinophyte abundance, was recorded in the summer.

Intensive growth of phytoplankton, mainly by the neritic forms of the centric diatoms mentioned, shows that the upper layers of Butrinti mainly belong to zone 3. According to Dutrieux and Guelorget (1988) this zone is characterized by limited impact of hydrodynamic conditions; the organic matter content increases in both sediment and water, although the overall living conditions remain good. It represents a habitat favourable for shellfish reproduction, as evidenced by profusion of *Mytilus galloprovincialis* everywhere in Butrinti. However, being permanently stratified with anoxic bottom waters, the lagoon poses a potential risk to aquaculture.

Centric diatoms were the most abundant in Orikumi (Miho and Dedej 1999). The phytoplankton structure seemed to be similar to that in Butrinti, but the cell density was much lower. However, the increase of peridinophytes was observed in summer as well. Taking the species composition into account, even Orikumi seems to represent predominantly zone 3, with similar features of surface waters in Butrinti, related to shellfish production. However, it is worth mentioning that the coastal wetland at Orikumi is exposed to one of the strongest human impacts among the Albanian lagoons. Its area was extremely reduced by land reclamation about 35 years ago. Consequently, its biological characteristics were significantly altered.

To obtain a complete zonation view for each lagoon a more detailed approach of their physico-chemical and biological features would be necessary. A small number of phytoplankton samples from Narta, a large and very shallow lagoon (the depth ranges from 0.3 to 1 m), contained a few species only. This water body is characterized by a very limited connection with the sea and slow water exchange, belonging mainly to zone 6. After Dutrieux and Guelorget (1988) it does not support intensive phytoplankton growth, and its use for intensive aquaculture is rather limited; therefore, the lagoon could be suitable for traditional fishing.

Pennate diatoms were most abundant in Karavasta. Unlike in other lagoons (Butrinti or Ceka), blooms or intensive growth of peridinophytes were not observed there. In agreement with Guelorget and Lefebvre (1993), zones 4 and 5 seem to prevail within the lagoon, characterised by a high productivity, mostly attributable to phytoplankton. Therefore, it may be used mainly in an extensive way for farming detritivorous fish species (e.g., mullet) or peneid shrimps (Dutrieux and Guelorget 1988). Similar characteristics seem to be typical of Patoku and Ceka (Lezha). As indicated by the diatom flora, dominated by centrics, Merxhani lagoon shows a relatively good water exchange with the sea, characteristic of zone 3.

During April-June 1987, an abnormal bloom of *Pseudonitzschia seriata* was observed in Butrinti, followed by a bloom of *Prorocentrum micans* and *P. minimum* (Miho 1994), both known to produce toxins (Hallegraeff 1995). Algal bloom was observed also in Ceka (Lezha; spring-summer 1992), where *Nitzschia* spp. or *Prorocentrum* spp. and *Gonyiaulax* spp. were dominant. This indicates conditions of stress, ensuing probably due to a combination of climate, the very limited water circulation in the lagoon and restricted water exchange with the sea. According to Marasovic (1989), the very high evaporation rate accompanied by increasing water temperature and salinity may contribute to the environmental stress as well. These critical conditions allow the presence of only a few species, with extremely dense growth.

Parameters important in evaluation of the trophic status and other ecological features of a habitat may include the diversity index (Shannon and Weawer 1949) and/or dominance index (McNaughton 1967). In Butrinti, the diversity index was higher in marine habitats (varying from 1.9 to 3.4 in the littoral zone) than within the lagoon (ranging from 0.6 to 2.5; Miho 1994, 1996). In lagoon habitats, contributions of the two dominant species were very high (up to 92.4 % in Butrinti) and showed a strong seaward decrease (27.8% in Armura or 30.3% in Saranda). Generally, even the number of species was higher in the littoral marine habitats than in the lagoons, where the water exchange was limited. Armura, Butrinti (northern part), Karavasta, and Merxhani were the most distinct habitats in terms of species richness and trophic status.

CONCLUDING REMARKS

Albanian coastal wetlands, exemplified by the habitats studied in Butrinti, Armura, Karavasta, Orikumi and Merxhani show a high diversity of diatoms. The species composition found in some lagoons provides evidence of relatively good water exchange with the sea and favourable conditions of the natural environment. Stress conditions were observed in some other localities. Algal blooms were sporadically observed in Butrinti and Ceka, especially during the summer. The blooms were formed by pennate diatoms, e.g., *Pseudonitzschia seriata* and *Nitzschia reversa,* and by a few peridinophytes some of which are known to produce neurotoxins. Highly stressing conditions seem to prevail for an extended period of time in Narta and Kenalla pond (Lezha). The eutrophic status and related stressing conditions there are probably the result of limited water exchange with the sea. Moreover, the Albanian coast and the wetlands continue to be endangered by tourism, urban and industrial wastewater pollution, etc.

Potentially, the Albanian coast is a valuable environmental asset, but there is an urgent need of responsible protection and management.

Taking appropriate measures in important and sensitive watershed areas will help to prevent damage to biodiversity and other natural values. Studies of the structure of diatom floras would provide additional information leading toward a better ecological approach of coastal ecosystems.

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Appendix

TABLE 1. Checklist of Diatoms Found in Albanian Coastal Wetlands

Key: A: Armura; B: Butrinti; C: Ceka; D: Durresi; K: Karavasta; Ke: Kenalla; L: Lalzi; Le: Lezha; M: Merxhani; N: Narta; O: Orikumi; P: Patoku; S: Saranda; Vl: Vlora; V: Viluni (see Fig. 1).

Note: The taxa labeled with 'Vl' were reproted by Protic (1907), 'D' and partly 'K' by Dedej (1994, 1995), 'A, B, C, L, Le, K, Ke, M. O, P, S, V' by Miho (1994, 1996), Miho and Dedej (1999), and Miho and Mitrushi (1999); data for unlabeled taxa are from the unpublished notes of A. Miho.

Bacillariophyceae: Centricae

Actinocyclus cf. *subtilis* (Gregory) Ralfs [S]
Actinocyclus ochotensis Jouse [A]
Actinocyclus octonarius Ehrenberg (= *A. ehrenbergii* Ralfs) [B]
Actinocyclus subtilis (Gregory) Ralfs [A, B, S]
Actinoptychus senarius (Ehrenberg)Ehrenberg [B]
Actinoptychus splendens (Shadbolt) Ralfs [M]
Amphitetras antediluviana Ehrenberg [B, K, O]
Asteromphalus heptactis (Brébisson) Ralfs [B, M]
Asteromphalus robustus Castracane [B]
Aulacoseira ambigua (Grunow) Simonsen [B]
Aulacoseira granulata (Ehrenberg) Simonsen [B, K]
Aulacoseira islandica (Mueller) Simonsen [L]
Bacteriastrum furcatum Shadbolt [B, Ke]
Bacteriastrium delicatulum Cleve [B; Ke]
Biddulphia pulchella Gray [A, B]
Cerataulina pelagica (Cleve) Hendey [K]
Cerataulina bergonii (Peragallo) Schuett [B, D]
Ceratulus turgidus (Ehrenberg) Ehrenberg [B, C, K, M, P]
Chaetoceros affinis Lauder [B]
Chaetoceros atlanticus Cleve [B, K]
Chaetoceros atlanticus var. *neapolitana* (Schroeder) Schuett [B, K, M]
Chaetoceros decipiens Cleve [B]
Chaetoceros densus Cleve [B, Le]
Chaetoceros diversus Cleve [B, D]
Chaetoceros insignis Proshkina-Lavrenko [D]
Chaetoceros lorenzianus Grunow [D]
Chaetoceros muelleri Lemmermann [Ke]
Chaetoceros peruvianus Brightwell [D]
Chaetoceros subtilis Cleve [B]
Chaetoceros teres Cleve [D]
Chaetoceros tortissimus Grunow [B]
Chaetoceros wighamii Brightwell [B]
Coscinodiscus cf. *curvatulus* Grunow var. *minor*[B]
Coscinodiscus nodulifer Schmidt [B, K]
Cyclotella aff. *choctawhatcheeana* Prasad [B, O, K]
Cyclotella cf. *hustedti* Jurilj [B]
Cyclotella meneghiniana Kützing [B, Le, O, D]
Cyclotella ocellata Pantocsek [B, O]
Cyclotella radiosa (Grunow) Lemmermann [B, K]
Cyclotella striata (Kützing) Grunow [B, P]
Cymatosira lorenziana Grunow [S]
Dactyliosolen blavyanus (Peragallo) Hasle [B, D, M, O]
Dactyliosolen fragilissimus (Bergon) Hasle [B, D, K, M, O]
Guinardia flaccida (Castracane) Peragallo [K]
Guinardia striata (Stolterfoth) Hasle (=*Rhizosolenia stolterfothii* Peragallo) [B]
Hemiaulus hauckii Grunow [B, D, M]
Hyalodiscus radiatus (O'Meara) Grunow [B, D, K, Le, O, P, V]
Hyalodiscus scoticus (Kützing) Grunow [B]
Leptocylindrus adriaticus Schroeder [B, K, O]
Leptocylindrus minimus Grunow [B]
Melosira moniliformis (Mueller) Agardh var. *moniliformis* [B, Le, M, O, P, V]
Melosira nummuloides Agardh [B, K, Ke, M, O, P]
Melosira sol (Ehrenberg) Kützing [S]
Melosira varians Agardh [B, K, Vl]
Odontella aurita (Lyngbye) Brébisson [B, K]
Odontella mobiliensis (Bailey) Grunow [B, K]
Porosira cf. *pseudodenticula* (Hustedt) Jouse [A]
Proboscia alata (Brightwell) Sundstroem (=*Rhizosolenia alata* Brightwell) [B, D, K, M, O]
Pseudosolenia calcar-avis (Schultze) Sundstroem [B, D]
Rhizosolenia imbricata var. *shrubsolei* (Cleve) Schroeder [B]
Skeletonema costatum (Greville) Cleve [K]
Thalassiosira lacustris Grunow var. *lacustris* [B, K]
Triceratium favus Ehrenberg [B]
Triceratium reticulum Ehrenberg [S]

Bacillariophyceae: Pennatae

Achnanthes brevipes Agardh var. *brevipes* [B, K]
Achnanthes brevipes var. *angustata* (Greville) Cleve [B, P]
Achnanthes brevipes var. *intermedia* (Kützing) Cleve [B, K,M, O, P, V]
Achnanthes cf. *groenlandica* (Cleve) Grunow [S]
Achnanthes delicatula (Kützing) Grunow var. *delicatula* [B]
Achnanthes exigua Grunow [B]
Achnanthes exilis Kützing [Vl]
Achnanthes hungarica Grunow [K]
Achnanthes lanceolata (Brébisson) Grunow agg. [B]
Achnanthes longipes Agardh [B, K, M, P, V]
Achnanthes minutissima Kützing [B, D, K, M, N, Vl]
Achnanthes separata Hustedt [A, S]
Achnathes parvula Kützing [S]
Adlafia minuscula Grunow (Lange-Bertalot) [Le]
Amphipleura pellucida (Kützing) Kützing [B, D, K, Vl]
Amphora angularis Gregory [Vl]
Amphora angularis var. *lyrata* Van Heurck [Vl]
Amphora arenaria Donkin [A]
Amphora *cf.* granulata *Gregory [S]*
Amphora *cf.* tomiakae *Witk., Lange-Bert. and Metz. [B, S]*

Amphora coffeaeformis (Agardh) Kützing [B, C, K, O, P]
Amphora commutata Grunow [Vl]
Amphora costata W. Smith [S]
Amphora holsatica Hustedt [B, D, Le, O, P]
Amphora inflata Grunow [K]
Amphora kolbei Aleem [A, S]
Amphora laevis Gregory [K]
Amphora laevissima Gregory [S]
Amphora lineolata Ehrenberg [B, K, Ke, M, Vl]
Amphora lybica Ehrenberg [B, D, K, O]
Amphora marina (W. Smith) Van Heurck [A, B]
Amphora ovalis (Kützing) Kützing [K, Le, O, Vl]
Amphora ovalis var. *affinis* Kützing [Vl]
Amphora pediculus (Kützing) Grunow [B, K, Le, Vl]
Amphora pseudohyalina Simonsen [S]
Amphora robusta Gregory [B, K, Le, P]
Amphora salina W. Smith [Vl]
Aneumastus tusculus (Ehrenberg) Mann [Le, Vl]
Brachysira serians (Brébisson) Round and D.G. Mann [Vl]
Ardissonia crystallina (Agardh) Grunow (Agardh) Kützing [A, B]
Ardissonia fulgens (Greville) Grunow [B, K, Le, P, S]
Asterionellopsis glacialis (Castracane) Round [K]
Bacillaria cf. *socialis* (Gregory) Ralfs [S]
Bacillaria paradoxa Gmelin [B, D, K, Le, P]
Berkeleya scopulorum (Brébisson) Cox [S]
Caloneis amphisbaena (Bory) Cleve [B, K]
Caloneis amphisbaena var. *subsalina* Van Heurck [Vl]
Caloneis bicuneata (Grunow) Wolle [B]
Caloneis liber (W. Smith) Hendey [B]
Caloneis silicula (Ehrenberg) Cleve agg. [B, D, K, Vl]
Caloneis westii (W. Smith) Hendey [B, K, P]
Campylodiscus bicostatus W. Smith [B, K, O]
Campylodiscus cf. *simulans* Gregory
Campylodiscus clypeus Ehrenberg [B, K, O, Vl]
Campylodiscus echeneis Ehrenberg [B, K, Le, P]
Campylodiscus levanderi Hustedt [B, K]
Campylosira cymbelliformis (Schmidt) Grunow [Vl]
Cavinula cocconeiformis (Gregory) Mann and Stickle [B, K]
Cocconeis costata Gregory [B, K, O]
Cocconeis guttata Hustedt [S]
Cocconeis molesta Kützing [K, Le]
Cocconeis neodiminuta Krammer [B, K, O]
Cocconeis pediculus Ehrenberg [B, O, Vl]
Cocconeis placentula (Ehrenberg) Hustedt agg. [Vl]
Cocconeis placentula Ehrenberg var. *placentula* [B, K, O]
Cocconeis placentula var. *euglypta* (Ehrenberg) Cleve [B, K, Le, P]
Cocconeis placentula var. *lineata* (Ehrenberg) Van Heurck [Le]
Cocconeis scutellum Ehrenberg [B, K, Le, P]
Cocconeis pseudomarginata Gregory [B, A]
Craticula cuspidata (Kützing) Mann [B, D, K, O]
Craticula halophila (Grunow) D.G. Mann [B, D, K, Le, V]
Ctenophora pulchella (Ralfs ex Kützing) Williams and Round (=*Fragilaria pulchella* (Ralfs) Lange-Bertalot [B, Le, K, O]
Cylindrotheca cf. *gracilis* (Brébisson) Grunow [B, K, P]
Cylindrotheca closterium (Ehrenberg) Reimann and Lewin (=*Nitzschia closterium* (Ehrenberg) W. Smith) [B, D, K, M, P]
Cymatopleura elliptica (Brébisson) W. Smith [B, Vl]
Cymatopleura solea (Brébisson) W. Smith [B, Vl]
Cymbella affinis Kützing agg. [B, K, O, P]
Cymbella ampicephala Naegeli var. *amphicephala* [B]
Cymbella aspera (Ehrenberg) Peragallo [Vl]
Cymbella cistula (Ehrenberg) Kirchner agg. [Vl]
Cymbella cymbiformis Agardh var. *cymbiformis* [Vl]
Cymbella delicatula Kützing [Vl]
Cymbella ehrenbergii Kützing [Vl]
Cymbella helvetica Kützing [B, P, Vl]
Cymbella lanceolata (Ehrenberg) Kirchner [Vl]
Cymbella pusilla Grunow [Vl]
Cymbella tumida (Brébisson) Van Heurck [K, P, Vl]
Cymbella turgida (Gregory) Cleve [B]
Delphineis cf. *livingstonii* Prasad [S]
Denticula tenuis Kützing [Vl]
Diatoma anceps (Ehrenberg) Kirchner [Vl]
Diatoma ehrenbergi Kützing [Le]
Diatoma hyemalis (Rith) Heiberg [Vl]
Diatoma tenuis Agardh (=*D. elongatum* (Lyngbye) Agardh) [O]
Diatoma vulgaris Bory var. *vulgaris* [B, Vl]
Diatoma vulgaris var. *tenuis* Van Heurck [Vl]
Dimerogramma minor (Gregory) Ralfs [S]
Diploneis cf. *interrupta* (Kützing) Cleve [S]
Diploneis cf. *littoralis* (Donkin) Cleve [B, S]
Diploneis cf. *mirabilis* Koenig [A]
Diploneis cf. *smithii* var. *dilatata* (Peragallo) Terry
Diploneis didyma (Ehrenberg) Cleve [B, Le, K, O, P]
Diploneis domblittensis Cleve [B]
Diploneis elliptica (Kützing) Cleve (=*Navicula elliptica* Kützing) [Vl]
Diploneis marginestriata Hustedt [B]
Diploneis oblongella (Naegeli) Cleve-Euler [B]
Diploneis ovalis (Hilse) Cleve [B, Ke]
Diploneis smithii var. *pumila* (Grunow) Hustedt [B, K, P]
Diploneis subovalis Cleve [B, M]
Diploneis vetula (Schmidt) Cleve [A]
Dploneis subcincta (Schmidt) Cleve [B]
Encyonema caespitosum (Kützing) Grunow [Vl]
Encyonema prostratum (Berkeley) Cleve [Vl]
Encyonema ventricosum Kützing [B, Vl]
Encyonopsis minuta Krammer and Reichardt [S]
Entomoneis paludosa (W. Smith) Reimer [B, K, Le, O, P]
Entomoneis alata (Ehrenberg) Ehrenberg [B, S]
Epithemia adnata (Kützing) Brébisson [B, K, O, Vl]
Epithemia smithii Carruthers [B]
Epithemia sorex Kützing [B, K, O, Vl]
Epithemia turgida (Ehrenberg) Kützing [Vl]
Epithemia turgida var. *granulata* (Ehrenberg) Grunow [Le]
Eunotia arcus Ehrenberg [Vl]
Eunotia cf. *exigua* (Brébisson) Rabenhorst [Le]
Eunotia flexuosa (Brébisson) Kützing [Vl]
Eunotia pectinalis (Dillwyn) Rabenhorst [Vl]
Eunotia praerupta Ehrenberg [B, K, O]
Fallacia versicolor (Grunow) Mann [S]

Fragilaria affinis Kützing [K]
Fragilaria capucina Grunow var. *capucina* [Vl]
Fragilaria capucina var. *perminuta* (Grunow) Lange-Bertalot [B]
Fragilaria crotonensis Kitton [B, D, K]
Fragilaria dilatata (Brébisson) Lange-Bertalot (=*F. capitata* (Ehrenberg) Lange-Bertalot) [Vl]
Fragilaria fasciculata (Agardh) Lange-Bertalot [B, K, Le, O. P. V]
Fragilaria investiens (W. Smith) A. Cleve [B]
Fragilaria laevissima Oestrup [B, S]
Fragilaria pinnata Ehrenberg gr. [B, K, O, P]
Fragilaria ulna (Nitzsch) Lange-Bertalot agg. [B, Le, O, P]
Fragilaria ulna (*Synedra*) var. *longissima* Van Heurck [Vl]
Fragilaria ulna (*Synedra*) var. *oxyrhynchus* (Kützing) Van Heurck [Vl]
Fragilaria (*Synedra*) *ulna* var. *subaequalis* Grunow [Vl]
Fragilaria virescens Ralfs [Vl]
Frustulia cf. *weinholdii* Hustedt [B]
Gomphonema acuminatum Ehrenberg [Le, Vl]
Gomphonema angustatum (Kützing) Rabenhorst [Vl]
Gomphonema angustum Agardh [Vl]
Gomphonema constrictum Ehrenberg [Vl]
Gomphonema gracile Ehrenberg [Le]
Gomphonema minutum (Agardh) Agardh agg. [B. K, O]
Gomphonema olivaceum (Horn.) Brébisson var. *olivaceum* [B, K, O, Vl]
Gomphonema olivaceum var. *calcareum* (Cleve) Cleve [B, K, O]
Gomphonema olivaceum var. *staurophorum* Pantocsek [B, D, K]
Gomphonema parvulum (Kützing) Grunow [Le, Vl]
Gomphonema pseudotenellum Lange-Bertalot [Le]
Gomphonema truncatum Ehrenberg [B, D, K, Le, O]
Grammatophora angulosa Ehrenberg var. *angulosa* [B, Le]
Grammatophora macilenta W. Smith [B, K, V]
Grammatophora oceanica (Ehrenberg) Grunow var. *oceanica* [B, K, Le, N, O, P, V]
Gyrosigma acuminatum (Kützing) Rabenhorst var. *acuminatum* [B, K, Le, N, P, V]
Gyrosigma attenuatum (Kützing) Rabenhorst [B, K, O]
Gyrosigma arcuatum (Donkin) Sterrenburg
Gyrosigma balticum (Ehrenberg) Rabenhorst [B, K, Le, N, O, P, V]
Gyrosigma cf. *obscurum* (W. Smith) Griffith and Henfrey [B]
Gyrosigma cf. *peisonis* (Grunow) Hustedt [Le]
Gyrosigma cf. *wansbecki* (Donkin) Cleve [Le]
Gyrosigma compactum (Grev.) Cleve [B, S]
Gyrosigma fasciola (Ehrenberg) Griff. and Henf. [B, K, Le, N, O, P, V]
Gyrosigma strigilis (W. Smith) Cleve [B, K, Le, P]
Hantzschia amphioxys (Ehrenberg) Grunow [B, Vl]
Hantzschia amphioxys fo. *capitata* Hustedt [B]
Licmophora cf. *grandis* (Kützing) Grunow [B, K]
Licmophora cf. *hyaline* Kützing [B, K]
Licmophora ehernberghii (Kützing) Grunow [B, K]
Licmophora flabellata var. *splendida* W. Smith [K]
Licmophora remulus Grunow [B, K, Le, N, O, P, V]
Licmophora dalmatica (Kützing) Grunow [Vl]
Licmophora flabellata (Carmichael) Agardh
Licmophora gracilis (Ehrenberg) Grunow
Licmophora paradoxa (Lyngbye) Agardh [A, S]
Lyrella amphoroides D.G. Mann [S]
Lyrella cf. *clavata* (Gregory) D.G. Mann [M]
Lyrella lyra (Ehrenberg) Karayeva [B, K]
Lyrella spectabilis (Gregory) D.G. Mann [A, S]
Lyrella sulcifera (Hustedt) Witkowski [B, K, O, P, Le]
Mastogloia angulata Lewis [B, K, O, P, Le]
Mastogloia binotata (Grunow) Cleve [B]
Mastogloia braunii Grunow [B, K, O, Vl]
Mastogloia cf. *adriatica* Voigt [B]
Mastogloia cf. *baldjikiana* Grunow [B, K]
Mastogloia cf. *biocellata* (Grunow) Nov. and Muft. [B]
Mastogloia cf. *labuensis* Cleve [B]
Mastogloia cf. *recta* Husted [B]
Mastogloia crucicula (Grunow) Cleve [B, K, O]
Mastogloia cuneata (Meister) Simonsen [B]
Mastogloia dansei Thwaites [Vl]
Mastogloia grunowii A. Schmidt [B]
Mastogloia ignorata Hustedt [B]
Mastogloia lanceolata Thwaites [A]
Mastogloia laterostrata Hustedt [B]
Mastogloia ovalis A. Schmidt [A]
Mastogloia paradoxa Grunow [B]
Mastogloia pseudoexigua Cholonky [B]
Mastogloia pseudolatecostata Yohn and Gibson [A]
Mastogloia pumila (Grunow) Cleve [B]
Mastogloia pusilla (Grunow) Cleve [B]
Mastogloia robusta Hustedt [B]
Mastogloia smithii Thwaites var. *smithii* [B]
Mastogloia smithii var. *lacustris* Grunow [B, D, K, O]
Mastogloia splendida (Gregory) Cleve [B]
Mastogloia vasta Hustedt [B]
Navicula agnita Hustedt [A]
Navicula arenaria Donkin [B, S]
Navicula cf. *besarensis* Giffen [S]
Navicula cf. *heimansii* Van Dam et Kooyman [B]
Navicula cf. *indulgens* Simonsen [B]
Navicula cf. *johanrossii* Giffen [S]
Navicula cf. *subhamulata* Grunow [Le]
Navicula cincta (Ehrenberg) Kützing [Vl]
Navicula cluthensis Gregory var. *cluthensis* [P, V]
Navicula cryptocephala Kützing [D, K, Vl]
Navicula cryptotenelloides Lange-Bertalot [B]
Navicula dealpina Lange-Bertalot [Vl]
Navicula digitoradiata (Gregory) Ralfs [Vl]
Navicula distans (W. Smith) Ralfs [Vl]
Navicula duerrenbergiana Hustedt [B]
Navicula erifuga Lange-Bertalot [A]
Navicula granulata Bailey [C, Ke, V]
Navicula gregaria Donkin [B, S, V]
Navicula integra W. Smith [Vl]
Navicula monilifera Cleve [B, K]
Navicula oblonga (Kützing) Kützing [B, K, O, Vl]
Navicula pavillardii Hustedt [B, C]
Navicula peregrina (Ehrenberg) Kützing [Vl]
Navicula perminuta Grunow [B]

Navicula perrhombus Hustedt [B]
Navicula phyllepta Kützing [B, K, O, P, Le]
Navicula phylleptosoma Lange-Bertalot [B]
Navicula pseudosilicula Hustedt [Vl]
Navicula radiosa Kützing [V, Vl]
Navicula recens (Lange-Bertalot) Lange-Bertalot [Le]
Navicula rhynchocephala Kützing [B, Vl]
Navicula rolandii Lange-Bert. and Witk. [O]
Navicula salinarum Grunow [B, K, O, Vl]
Navicula salinicola Hustedt [A, B, S]
Navicula termes Ehrenberg [Vl]
Navicula tripunctata (Mueller) Bory [B, Le]
Navicula veneta Kützing [B, K]
Navicula viridula (Kützing) Ehrenberg [Vl]
Neidium iridis var. *affinis* Ehrenberg [Vl]
Neidium iridis var. *amphirhynchus* Ehrenberg [Vl]
Nitzschia acicularioides Hustedt [S]
Nitzschia amphibia Grunow [B]
Nitzschia angularis W. Smith [A, S]
Nitzschia cf. *filiformis* var. *conferta* [Le]
Nitzschia cf. *graeffii* Grunow [S]
Nitzschia cf. *plana* W. Smith [B, S]
Nitzschia cf. *prolongata* Hustedt [B]
Nitzschia cf. *splendida* Kützing [B, K]
Nitzschia capitellata Hustedt [B, K, O]
Nitzschia circumsuta (Bailey) Grunow [B, D, K, P, Le, V]
Nitzschia clausii Hantzsch [B]
Nitzschia coarctata Grunow [B, K, O, P, Le]
Nitzschia communis Rabenhorst [Vl]
Nitzschia commutata Grunow [Vl]
Nitzschia compressa (Bailey) Boyer var. *compressa* [B, D, K, O, P, Le]
Nitzschia constricta (Kützing) Ralfs [B, D, K, O, P, Le]
Nitzschia denticula Grunow (=*Denticula Kützingii* Grunow) [B, K, O, P]
Nitzschia dissipata (Kützing) Grunow [B]
Nitzschia dissipata var. *media* (Hantzsch) Grunow [Le]
Nitzschia distans var. *tumescens* Gregory [K]
Nitzschia filiformis (W. Smith) Hustedt [A, B, S]
Nitzschia flexoides Geitler [B]
Nitzschia fossilis Grunow [Le]
Nitzschia granulata Grunow [B, Le]
Nitzschia hungarica Grunow [Vl]
Nitzschia incospicua Grunow [B]
Nitzschia lacuum Lange-Bertalot [A, B, S]
Nitzschia lanceola var. *minutula* Grunow [B]
Nitzschia lanceolata W. Smith [B]
Nitzschia linearis (Agardh) W. Smith [Vl]
Nitzschia littoralis Grunow [S]
Nitzschia longissima (Brébisson) Ralfs [B, D, K, Le, V]
Nitzschia macilenta Gregory [B]
Nitzschia microcephala Grunow [Le]
Nitzschia palea (Kützing) W. Smith [B, K, Le, Vl]
Nitzschia panduriformis Gregory [A]
Nitzschia pararostrata (Lange-Bertalot) Lange-Bertalot [B]
Nitzschia recta Hantzsch [B]
Nitzschia reversa W. Smith [Le, O]
Nitzschia scalpelliformis Grunow [V]
Nitzschia sigma (Kützing) W. Smith [B, K, Le, Vl]
Nitzschia sigma var. *sigmatiella* Grunow [D, K, Le, P, V]
Nitzschia sigmoidea (Nitzsch) W. Smith [Vl]
Nitzschia paleacea (Grunow) Grunow [Vl]
Nitzschia vitrea var. *salinarum* Grunow [Vl]
Opephora mutabilis (Grunow) Sabbe and Vyverman [B]
Parlibellus berkeleyi (Kützing) Cox [A, S]
Parlibellus cruciculoides (Brock.) Witk., Lange-Bert. and Metzeltin [S]
Parlibellus protracta (Grunow) Witk., Lange-Bert. and Metzeltin [A, Le, S]
Parlibellus rhombicula (Hustedt) Witk., Lange-Bert. and Metzeltin [S]
Petroneis humerosa (Brébisson) D.G. Mann [B, K, M]
Pinnularia appendiculata (Agradh) Cleve [Vl]
Pinnularia gibba Ehrenberg [Vl]
Pinnularia legumen (Ehrenberg) Ehrenberg [Vl]
Pinnularia major (Kützing) Rabenhorst [Vl]
Pinnularia microstauron var. *brebissonii* (Kützing) Mayer [Vl]
Pinnularia nobilis (Ehrenberg) Ehrenberg [Vl]
Pinnularia pulchra Oestrup Ehrenberg) [Vl]
Pinnularia tabellaria Ehrenberg [Vl]
Placoneis elginensis (Gregory) Cox [Vl]
Placoneis gastrum var. *signata* (Hustedt) [B, K]
Plagiotropis gibberula Grunow [S]
Plagiotropis lepidoptera (Gregory) Kuntze [A, B, V]
Pleurosigma angulatum (Quekett) W. Smith [B, K, Le, O, P, V]
Pleurosigma cf. *rostratum* Hustedt [M]
Pleurosigma elongatum W. Smith [B, D, K, Le, O, P, V]
Pleurosigma formosum Peragallo [B, K, Le, O, P, V]
Pleurosigma salinarum Grunow [S, Le]
Pseudonitzschia delicatissima (Cleve) Peragallo [D]
Pseudonitzschia seriata (Cleve) Peragallo [B, K, Le, O, P, V]
Pterodictyon gemma (Ehrenberg) D.G. Mann [B, K, P]
Rhabdonema adriaticum Kützing [B, K, Le, O, P, V]
Rhoicosphenia abbreviata (Agardh) Lange-Bertalot [B, Vl]
Rhoicosphenia marina (W. Smith) M. Schmidt [B]
Rhopalodia acuminata Krammer [A, S]
Rhopalodia brebissonii Krammer [B]
Rhopalodia cf. *constricta* (W. Smith) Krammer [A]
Rhopalodia cf. *gibberula* (Ehrenberg) Mueller [B, K]
Rhopalodia gibba (Ehrenberg) Mueller [B, K, Le, O, P, Vl]
Rhopalodia gibba var. *minuta* Krammer [A, S]
Rhopalodia musculus (Kützing) Mueller [B, D, K, Le, O, P, V]
Sellaphora bacillum (Ehrenberg) Mereschkowsky [Vl]
Sellaphora seminulum (Grunow) D.G. Mann [Vl]
Seminavis basilica Danielidis and D.G. Mann [A, B, S]
Stauroneis acuta W. Smith [Vl]
Stauroneis anceps Ehrenberg [Vl]
Stauroneis gregori Ralfs [Vl]
Stauroneis phoenicenteron Ehrenberg [Vl]
Stauroneis salina W. Smith [Vl]
Staurosira brevistriata Grunow (=*Fragilaria brevistriata* Grunow, *Pseudostaurosira brevistriata* (Grunow) Williams and Round) [B, O]
Staurosira construens Ehrenberg (=*Fragilaria construens*

(Ehrenberg) Grunow) [B, S]
Striatella unipunctata (Lyngbye) Agardh [B, K, Le, O, P, V]
Surirella biseriata Brébisson [Vl]
Surirella brebissonii Krammer and Lange-Bertalot [B, K, O]
Surirella cf. *fluminensis* Grunow [B, K, M, P]
Surirella cf. *scalaris* Giffen [A, S]
Surirella fastuosa (Ehrenberg) Kützing [B, K, Le, O, P, V]
Surirella minuta Brebisson [Vl]
Surirella ovalis Brébisson [B, K, O, Vl]
Surirella spiralis Kützing [K, Vl]
Surirella splendida (Ehrenberg) Kützing [Vl]
Surirella striatula Turpin [B, C, K, O, P]
Synedra tabulata (Agardh) Kützing var. *tabulata* [B, K, Le]
Synedra undulata (Bailey) Gregory (=*Toxarium undulatum* Bailey) [B, Le, O]
Tabellaria fenestrata (Lyngbye) Kützing [Vl]
Tabellaria flocculosa (Roth) Kützing [Vl]
Thalassionema nitzschioides (Grunow) Grunow [B, D, K, Le, O]
Trachyneis aspera (Ehrenberg) Cleve [A]

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Marrying Taxonomy and Ecology: An Attempt

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Freshwater diatoms present an interesting challenge in an era when biodiversity is becoming a major concern. Although tremendously useful indicators of ecological conditions, past and present, lack of taxonomic knowledge limits the potential of ecological interpretation. At the same time the ecological studies that are carried out provide less than optimal feedback to the taxonomic literature. I suggest that appropriate use of available computer-based technologies can integrate these fields to the benefit of both. I further outline the approaches taken in an early and primitive attempt to accomplish this goal, the benefits derived, and the mistakes made and inadequacies of our effort at that time. Thoughtful application of technologies now available has the potential to further integrate studies and expand eventual understanding.

The following is a discussion of an attempt to marry the fundamental approaches of systematic practice to ecological studies. The tools and approaches used are, in retrospect, quite primitive, but there is an underlying logical framework that applies to all such endeavors, in taking on any problem at any time. I hope that discussing the way we attempted to solve problems common to any taxonomically based diatom study, what worked and what didn't, and the mistakes made, will be of some value to current investigators.

I should hasten to explain that the "we" in the previous paragraph is used advisedly. I am not a programmer, so much of the development and implementation was done by other people, better equipped to deal with the intricacies of programming than I. I thank the late Dr. Vincent Noble and Dr. Edward Johnston (Johnston and Stoermer 1976) for enlightening discussions of logical structures appropriate for human — computer interactions. The initial programming was done by Dr. J.K.C. Huang and the system was brought to its most advanced state largely through the efforts of Theodore and Barbara Ladewski (Ladewski and Stoermer 1973; Sicko-Goad et al. 1977). Numerous helpful comments and suggestions were also made by many technical staff and students, which materially helped shape the project.

THE PROBLEM

In the mid 1960s I was a young investigator faced with the rather intimidating problem of investigating the algal flora of the Laurentian Great Lakes. At the time, severe eutrophication problems were apparent in many regions of these lakes (Beeton 1965, 1969). Because of the Great Lakes' tremendous value to the economies of the United States and Canada, considerable resources were available for studies related to water quality. Many of the practical problems that beset the lakes at that time were directly related to algae. Taste and odor problems caused by diatoms in the spring (Vaughn 1961, 1962) and cyanophytes in the summer and fall (Stoermer and Stevenson

1980; Bierman and Dolan 1981; Stoermer and Theriot 1985). *Cladophora* was a nuisance in many regions of the lakes (Wolfe and Sweeney 1980) and generally unpleasant obnoxious conditions were present in many areas. Lake Erie, in particular, became a cause célèbe of the environmental activism of the day, and was widely reported in the common press to be a "dead lake." This was somewhat problematic to biologists, as the actual problem was over-production, which eventually led to de-oxygenation of the bottom waters in certain areas of the lakes, creating so called "dead zones" where benthic invertebrates were periodically exterminated. In retrospect, the problems of the 1960s and 1970s were only the most recent in a long history of environmental catastrophes, such as epidemics of water-borne diseases (Beatty 1982; Bonner 1991) that devastated communities that drew drinking water from the lakes. For example, the great cholera epidemic of 1854 was estimated to have killed five percent of the total population of the city of Chicago. Collapse of native fish stocks began soon after western settlement of the region (Smith 1972), and culminated in total extermination of some native stocks by 1950 (Beeton 1969) and introduction of many exotic fish species.

One would rationally suppose such a valuable, but clearly damaged, ecosystem would have received careful and comprehensive study, especially considering the large number of well-known academic institutions in the region. Unfortunately, this was not the case. The ecological history of the Great Lakes, in many respects, provides a sterling example of precisely the wrong way to approach management of a large and complex ecosystem. Each successive crisis generated a wave of "directed research" centered on the apparent problem and to a lesser extent, if at all, on its root causes. "Charismatic vertebrates," in this case fish, were the initial center of attention, and lesser attention and resources were devoted to the rest of the biota or to chemical and physical factors of the environment.

In the case of diatoms, early (in the North American context) exploratory studies were carried out by J.W. Bailey in 1839, first mentioned in 1842 (Bailey 1842a, 1842b), and sent to C.G. Ehrenberg, who more formally published them in his monumental works (Ehrenberg 1845, 1854). These collections are still maintained at the Museum für Naturkunde, Humboldt-Universität zu Berlin, and have been used in more recent studies of the Great Lakes diatom flora (Stoermer and Ladewski 1982). Early pollution studies, particularly in the area of Chicago (Thomas and Chase 1887) and Cleveland (Vorce 1881, 1882) produced collections which are still available, but the majority of taxonomic work undertaken was either un-vouchered, or the material resulting from the study has been lost. For example, studies on early fisheries declines included some work on diatoms (e.g., Ward 1896; Thompson 1896) but we have never been able to locate any of these collections.

Thus, from the beginning it was apparent that the type of supporting references and materials generally assumed to be available to ecological studies were lacking. Although this problem is obvious in the Great Lakes case, it applies to the majority of studies attempting to use diatoms as ecological indicators, as I have argued elsewhere (Stoermer 2001).

APPROACH

Collections

Early on I determined that it was absolutely necessary to maintain a consistent and reasonably well ordered reference collection. It was clear that the available literature of the time was grossly insufficient to support repeatable identifications, so the availability of a reference standard was essential. Maintenance of vouchers, once a routine part of good scientific practice, has largely been abandoned in ecological studies. Logically, it is still necessary for studies involving lesser-known organism groups, and certainly should be a requirement for studies involving diatoms. It is sometimes argued that maintaining collections is "too expensive" for the competitive world of ecological funding. In a reasonable and logical world the functions of developing a comprehensive taxonomy might be separated, as they are in most large organisms, but this was not the case at the time I began. Although it has become much easier in recent years, due to general recognition of the biodiversity crisis, in the 1960s and 1970s it was virtually impossible to obtain direct funding for taxonomic studies of microscopic eukaryotes.

In our case, I simply made the decision that studies from our lab would be supported by vouchers, as a minimum standard of scientific practice. Our collections are in the form of lots, numbered consecutively. Each lot consists of raw material, cleaned material, and one or more slides. In some cases, we have accepted slides from other investigators and integrated them into the collection without other material, but this is a compromise to be avoided if at all possible. Because we operated primarily from ships, locality information consists of latitude and longitude and brief habitat and collection method descriptors. With the current availability of global positioning system (GPS) apparatus, there is now no excuse not to substitute this unambiguous information for references to inconstant physical landmarks and place names. In the better systems available, it is also possible to directly transcribe information electronically, avoiding the inevitable mistakes introduced by hand transcription.

Index and Pictorial Reference

When working on a system such as the Great Lakes it is easy to escape the illusion that appropriate names for all diatoms encountered exist in the literature, or the equally pernicious assumption that all names in the literature reflect biological reality. For that reason, we have always treated diatom names as entirely arbitrary. Thus, a nomenclaturally correct binomial is quite acceptable but, in our system, an arbitrary name (e.g., aff. *Navicula ambigua*) or a numerical designation (e.g., *Nitzschia* 343) is equally acceptable, *if it is supported by an adequate illustration and voucher specimen*. This, of course, is a compromise, recognizing the fact that it is not possible to resolve all taxonomic questions while conducting ecological studies, which furnished support for our lab at the time the system was instituted. In order to keep internal consistency, but avoid the extra time and effort necessary to directly compare specimens under a microscope, we resorted to a photographic archive. An illustration of the file used is shown in Figure 1. The elements are an epithet (upper left), one or more photographs (upper right), the dimensions of the specimen(s) (center) and coordinates of their location on a slide (in parentheses) taken from a particular microscope indicated by the letter following. Pictorial representations of specimens circled on a slide, and location of specimen(s) within a particular circle (lower left), photo magnification (lower center) and the collection number (lower right) are also provided. In our original system, additional notes were written on the back of

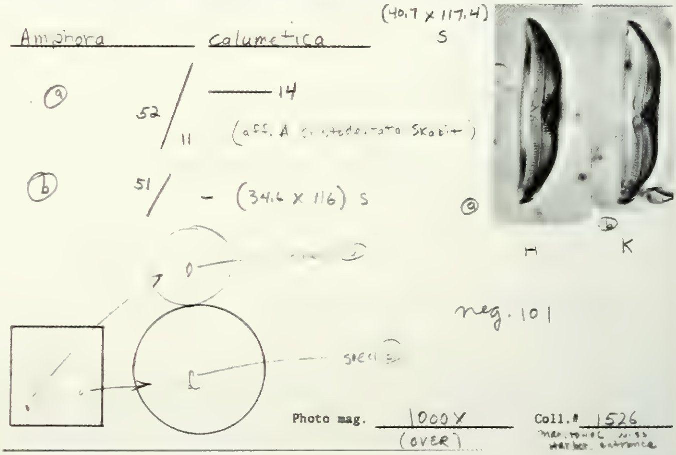
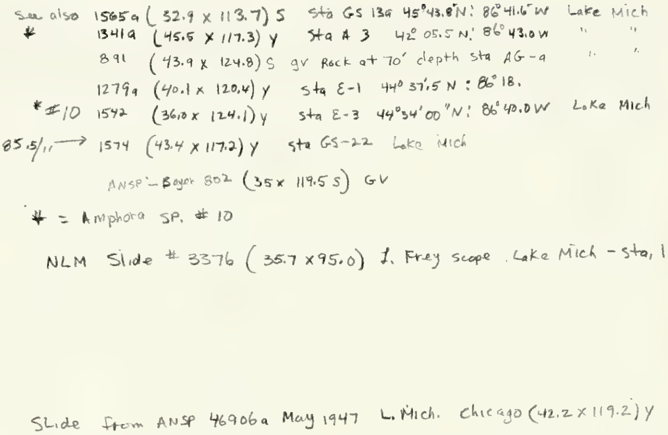


FIGURE 1. Example of card image used for specimen location and identification. See text for explanation.

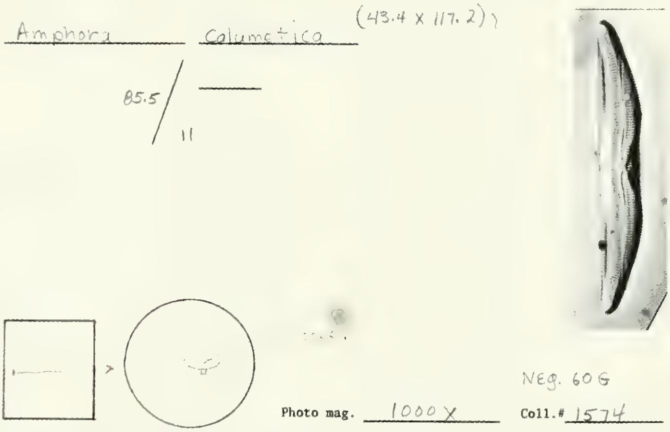
the card (Fig. 2). More than one card could be used to illustrate morphological variation and size series of any given entity (Fig. 3). Of course this is all very primitive, given the current availability of excellent databases that easily incorporate such information and are very easy to use. An example is the Filemaker™ template developed by Joynt (Joynt and Wolfe 1999) that can incorporate all these features and considerably more. The really important aspect of using such a system, rather than relying entirely on the published literature is that it allow one to follow the dictum of "when in doubt, sort it out." In the case of the Great Lakes, it was obvious that many "common species" had different morphotypes that had separate distribution patterns (Pappas and Stoermer 2001), and likely were genetically separate entities. Although separation of taxa on minor morphological variations might seem risky, in terms of supporting ecological interpretation, it is vastly less destructive than under-classification (Birks 1994). In fact, most multivariate statistical techniques will, given that identification is consistent, merely re-aggregate false separations.



See also 1565a (32.9 x 113.7) S Sta GS 139 45°43.8'N: 86°41.6'W Lake Mich
* 1341a (45.5 x 117.3) y Sta A 3 42° 05.5 N: 86° 43.0 W " "
891 (43.9 x 124.8) S gv Rock at 70' depth sta AG-9 " "
1279a (40.1 x 120.4) y sta E-1 44° 37'.5 N : 86° 18.
*#10 1542 (36.0 x 124.1) y sta E-3 44°34'00"N: 86°40.0W Lake Mich
85.5/11 → 1574 (43.4 x 117.2) y sta GS-22 Lake Mich
ANSP – Boyer 802 (35 x 119.5 S) GV
* = Amphora sp. # 10
NLM Slide # 3376 (35.7 x 95.0) 1. Frey scope . Lake Mich – sta, 1

Slide from ANSP 46906a May 1947 L. Mich. Chicago (42.2 x 119.2) y

FIGURE 2. Notes from reverse of card shown in Figure 1. Because *Amphora calumetica* is relatively rare, emphasis is on locating a range of specimens.



Amphora calumetica (43.4 x 117.2)
85.5/11
Neg. 60 G
Photo mag. 1000 X
Coll.# 1574

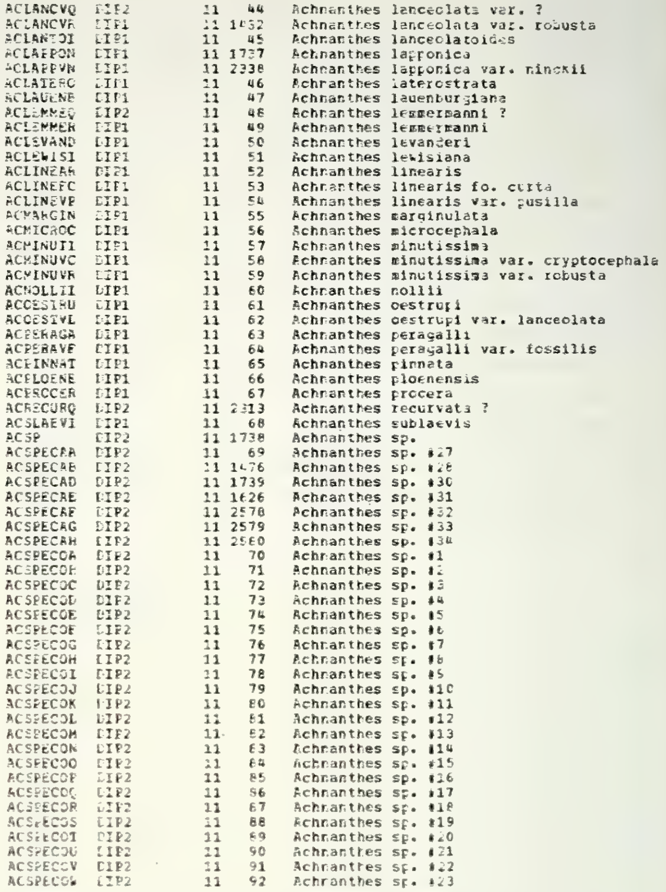
FIGURE 3. Example of an ancillary card, showing largest specimen of *A. calumetica* found at the time.

Computerization

In our case, computerization began as a simple data analysis problem. When handling large data sets, verification and data integrity are always problems, and ones that humans seem to handle poorly. Remembering these were the days when computer memories were limited and storage devices primitive. We had quite a struggle with programmers to use names recognizable to humans, and let the computer do the lookup, rather than simplifying the programmer's task by using a simple sequential list of taxa. Although this seems trivial in the modern context, I think there is an important lesson. Let computers do the simple, purely logical tasks. Save the human ability to deal with more complex tasks, perhaps aided by calculating engines, for the hard parts.

From this humble beginning, we, largely through the efforts of Theodore and Barbara Ladewski, were able to develop in integrated database system useful to both taxonomy and ecology. The program's name, through its several incarnations, was FIDO (a programmer's play on the word "phyto"). It consisted of the following elements:

MASTERLIST — A list of all acceptable names. These could be in the form of proper Latin binomials, binomials of convenience, or simple numerical or other arbitrary designation. The important part was that in order to become part of Masterlist, any designation had to be supported by a marked specimen in the collection and a photographic illustration in the master card file. Of course, all of these functions can be incorporated in any modern database. An sample portion is shown in Figure 4.



```
ACLANCVQ  DIP2        11   44   Achnanthes lanceolata var. ?
ACLANCVR  DIP1        11 1452   Achnanthes lanceolata var. robusta
ACLANTOI  DIP1        11   45   Achnanthes lanceolatoides
ACLAPPON  DIP1        11 1737   Achnanthes lapponica
ACLAPPVN  DIP1        11 2338   Achnanthes lapponica var. ninckii
ACLATERO  DIP1        11   46   Achnanthes laterostrata
ACLAUENB  DIP1        11   47   Achnanthes lauenburgiana
ACLEMMEQ  DIP2        11   48   Achnanthes lemmermanni ?
ACLEMMER  DIP1        11   49   Achnanthes lemmermanni
ACLEVAND  DIP1        11   50   Achnanthes levanderi
ACLEWISI  DIP1        11   51   Achnanthes lewisiana
ACLINEAR  DIP1        11   52   Achnanthes linearis
ACLINEFC  DIP1        11   53   Achnanthes linearis fo. curta
ACLINEVP  DIP1        11   54   Achnanthes linearis var. pusilla
ACMARGIN  DIP1        11   55   Achnanthes marginulata
ACMICROC  DIP1        11   56   Achnanthes microcephala
ACMINUTI  DIP1        11   57   Achnanthes minutissima
ACMINUVC  DIP1        11   58   Achnanthes minutissima var. cryptocephala
ACMINUVR  DIP1        11   59   Achnanthes minutissima var. robusta
ACNOLLII  DIP1        11   60   Achnanthes nollii
ACOESTRU  DIP1        11   61   Achnanthes oestrupi
ACOESTVL  DIP1        11   62   Achnanthes oestrupi var. lanceolata
ACPERAGA  DIP1        11   63   Achnanthes peragalli
ACPERAVF  DIP1        11   64   Achnanthes peragalli var. fossilis
ACPINNAT  DIP1        11   65   Achnanthes pinnata
ACPLOENE  DIP1        11   66   Achnanthes ploenensis
ACPROCER  DIP1        11   67   Achnanthes procera
ACRECURQ  DIP2        11 2313   Achnanthes recurvata ?
ACSLAEVI  DIP1        11   68   Achnanthes sublaevis
ACSP      DIP2        11 1738   Achnanthes sp.
ACSPECAA  DIP2        11   69   Achnanthes sp. #27
ACSPECAB  DIP2        11 1476   Achnanthes sp. #28
ACSPECAD  DIP2        11 1739   Achnanthes sp. #30
ACSPECAE  DIP2        11 1626   Achnanthes sp. #31
ACSPECAF  DIP2        11 2578   Achnanthes sp. #32
ACSPECAG  DIP2        11 2579   Achnanthes sp. #33
ACSPECAH  DIP2        11 2580   Achnanthes sp. #34
ACSPECOA  DIP2        11   70   Achnanthes sp. #1
ACSPECOB  DIP2        11   71   Achnanthes sp. #2
ACSPECOC  DIP2        11   72   Achnanthes sp. #3
ACSPECOD  DIP2        11   73   Achnanthes sp. #4
ACSPECOE  DIP2        11   74   Achnanthes sp. #5
ACSPECOF  DIP2        11   75   Achnanthes sp. #6
ACSPECOG  DIP2        11   76   Achnanthes sp. #7
ACSPECOH  DIP2        11   77   Achnanthes sp. #8
ACSPECOI  DIP2        11   78   Achnanthes sp. #9
ACSPECOJ  DIP2        11   79   Achnanthes sp. #10
ACSPECOK  DIP2        11   80   Achnanthes sp. #11
ACSPECOL  DIP2        11   81   Achnanthes sp. #12
ACSPECOM  DIP2        11   82   Achnanthes sp. #13
ACSPECON  DIP2        11   83   Achnanthes sp. #14
ACSPECOO  DIP2        11   84   Achnanthes sp. #15
ACSPECOP  DIP2        11   85   Achnanthes sp. #16
ACSPECOQ  DIP2        11   86   Achnanthes sp. #17
ACSPECOR  DIP2        11   87   Achnanthes sp. #18
ACSPECOS  DIP2        11   88   Achnanthes sp. #19
ACSPECOT  DIP2        11   89   Achnanthes sp. #20
ACSPECOU  DIP2        11   90   Achnanthes sp. #21
ACSPECOV  DIP2        11   91   Achnanthes sp. #22
ACSPECOW  DIP2        11   92   Achnanthes sp. #23
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FIGURE 4. A fragment of MASTERLIST printed in the late 1970s. Reading from the left, identity code, a major group and habitat code, two columns of numerical book keeping codes used by the program, and accepted epithets. At present, only about 20% of arbitrary numerical designations have been identified with described species,

DECKCHECK — a subprogram that checked all entries for codes not acceptable to Masterlist (coding violations, misspellings, etc.) and "suspicious" data. I am surprised at how few current databases include extended data verification protocols. It is our experience that an appreciable error rate is associated with human data entry and review, no matter how careful the analyst or transcriber, and many of these can be detected by fairly simple data screening protocols.

TAPEIT — A subprogram that wrote files for further processing and a separate permanent archive.

FETCH — A subprogram that retrieved data from the archive, either as hardcopy with summary statistics (subprogram ANALYZE) or output for further manipulation. An example of the former is shown in Figure 5. Note that summary statistics are calculated, including error estimates on counts. A separate, parallel-running system was used to collect and process chemical and physical data. This system was structured similarly to FIDO, which made merging of the databases for analysis relatively simple (Fig. 6). Examples of further manipulations include such things as distribution maps (Fig. 7) and representations of community structure based on multivariate statistical analyses (Figs. 8 and 9).

In the discussion above readers will note that almost all the design criteria were motivated by trying to bring some sort of modern taxonomic understanding to relatively large scale ecological

```
                          Southern Lake Michigan, August 1971

                  project:   SLM                  survey number:    5                      slide ID:  201
                     year:  1971                    Julian day: 236 (24 Aug)          sample number:  967
                  station:   201                         depth:   0.0 m             volume filtered:   50. ml
                 latitude:    42° 22.0'              longitude:  86° 18.0'          filter diameter:    2.00 cm
number of cells counted:  1063          volume of water scanned:    1.432 ml           field width:    0.0150 cm
                                                                                number of half-rows:    6
               diversity:      2.683                      evenness:   0.643


                                      number of
          division                     species  cells/ml     SE     CV   % pop.

   Cyanophyta (blue-green algae) . .       5      180.1     8.2  0.05  17.635
   Chlorophyta (green algae) . . . .      16      104.0     3.0  0.03  10.185
   Bacillariophyta (diatoms) . . . .      36      543.8     9.3  0.02  53.247
   Chrysophyta (chrysophytes). . . .       4       12.6     0.4  0.03   1.230
   Cryptophyta (cryptomonads). . . .       1        4.9     0.2  0.04   0.478
   Pyrrophyta (dinoflagellates). . .       2       25.1     0.9  0.03   2.461
   other . . . . . . . . . . . . . .       0        0.0     0.0  ****   0.0
   undetermined. . . . . . . . . . .       1      150.8     1.6  0.01  14.764
   total                                  65     1021.4     9.9  0.01 100.000
                                                                                   species  type          half-row counts
          species name                         cells/ml     SE     CV   % pop.      code    code   (1)   (2)   (3)   (4)   (5)   (6)

   Cyclotella stelligera . . . . . . . . . . .    280.0     2.5  0.01  27.409      CYSTELLI DIR1    80    62    67    73    55    68
   Undetermined flagellate spp.. . . . . . . .    150.8     1.6  0.01  14.764      FLSPP    UNS3    41    29    39    43    33    31
   Anacystis thermalis . . . . . . . . . . . .    122.9     3.1  0.03  12.030      AYTHERMA BGC1    48    18    34    29    19    28
   Fragilaria crotonensis. . . . . . . . . . .     65.6     5.4  0.08   6.425      FRCROTON DIP1    23    49    18     0     0     4
   Oocystis sp. #1 . . . . . . . . . . . . . .     58.6     2.1  0.04   5.742      OOSPECOA GRC2    19     2    18    21    16     8
   Anabaena flos-aquae . . . . . . . . . . . .     53.1     8.7  0.16   5.195      ABFLOSAQ BGF1     1     0     0     0    75     0
   Stephanodiscus minutus. . . . . . . . . . .     42.6     1.2  0.03   4.170      STMINUTU DIR1    13    14     6    13    11     4
   Cyclotella michiganiana . . . . . . . . . .     36.3     0.8  0.02   3.554      CYMICHIG DIR1    13    10     9     8     6     6
   Glenodinium sp. #1. . . . . . . . . . . . .     24.4     0.8  0.03   2.392      GDSPECOA DNS2     4     4     6     5    11     5
   Asterionella formosa. . . . . . . . . . . .     19.5     1.3  0.07   1.914      ASFORMOS DIP1     2     3     9     2    12     0
   Rhizosolenia gracilis . . . . . . . . . . .     16.8     1.2  0.07   1.640      RHGRACIL DIR1     5    11     3     5     0     0
   Fragilaria capucina . . . . . . . . . . . .     12.6     1.8  0.15   1.230      FRCAPUCI DIP1     2    16     0     0     0     0
   Crucigenia quadrata . . . . . . . . . . . .     11.2     1.9  0.17   1.094      CUQUADRA GRC1     0     0     0     0     0    16
   Nitzschia holsatica . . . . . . . . . . . .      9.1     1.5  0.17   0.889      NIHOLSAT DIP1     0     0     0    13     0     0
   Dinobryon cysts . . . . . . . . . . . . . .      8.4     0.4  0.04   0.820      DNCYSTS  CHS3     4     1     3     1     2     1
   Cyclotella comta. . . . . . . . . . . . . .      7.7     0.4  0.05   0.752      CYCOMTA  DIR1     4     1     1     0     3     2
   Nitzschia palea . . . . . . . . . . . . . .      7.0     0.2  0.03   0.684      NIPALEA  DIP1     1     1     1     2     3     2
   Scenedesmus sp. #2. . . . . . . . . . . . .      5.6     0.1  0.03   0.547      SCSPECOB GRC2     2     2     1     1     1     1
   Cyclotella comta var. bodanica. . . . . . .      4.9     0.3  0.07   0.478      CYCOMTVB DIR1     1     3     1     2     0     0
   Cryptomonas cyst. . . . . . . . . . . . . .      4.9     0.2  0.04   0.478      CZCYST   CRS3     2     1     1     2     1     0
   Nitzschia acicularis. . . . . . . . . . . .      4.9     0.1  0.02   0.478      NIACICUL DIP1     1     1     1     1     2     1
   Ankistrodesmus sp. #3 . . . . . . . . . . .      4.2     0.5  0.11   0.410      AKSPECOC GRC2     0     0     4     0     2     0
```

FIGURE 5. Example of ANALYZE output taken from a study of whole phytoplankton (diatoms and other groups) in southern Lake Michigan in 1971. Raw data are shown in right hand columns. Summarized data are shown in left columns. The large "undetermined" category consists mostly of microflagellates that cannot be satisfactorily identified with light microscopy.

projects, lacking the sort of traditional floristic and monographic support generally assumed. Perhaps more importantly, once our national science funding establishment began to awake to the fact that we are living in an ecosystem that is probably less than 20% described, this type of data base made it possible to attack some real taxonomic problems, particularly of the Great Lakes region (e.g., Theriot and Stoermer 1984, 1986).

MISTAKES AND PROBLEMS

In retrospect, it is nearly always possible to identify mistaken directions and things that should have been done differently. In our case the worst problems were partially our own fault and partially due to faults in the system. Part of the problem was that we started early in the game. Many diatomists resisted computer applications when they first became available. On the other hand, the funding agencies we dealt

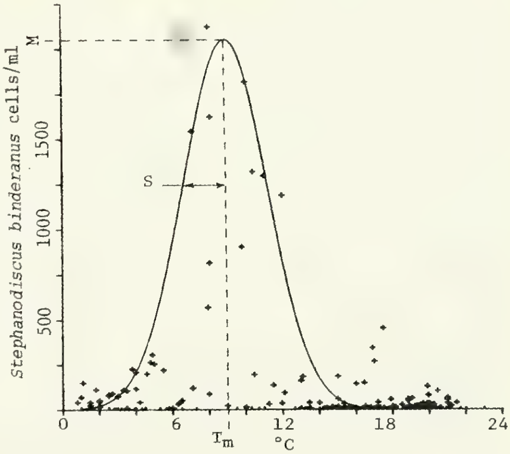

FIGURE 6. Example of data plotted from the study cited in Figure 5, in this case the absolute abundance of *Stephanodiscus binderanus* (Kütz.) Krieg relative to temperature (Stoermer and Ladewski 1976). Curve is fitted to data envelope and estimates of maximum abundance (M) and dispersion (S) are derived. Anomalous appearing points on the right come from inshore stations in the fall when populations are injected into the still warm lake from more rapidly cooling streams.

with at the time were reluctant to provide support dedicated to database development at the local project level. Some spent inordinate amounts of money on commercial database development, but most of these were put together with minimal inputs from the user community and, although they might have incorporated the latest programming tricks of the time, were hideously clumsy and inefficient to use. It has been my observation that most really useful databases incorporate a high level of specific user input, and most really successful programs are locally developed. Since computerization has become popular our national funding agencies have devoted considerable resources to development of several generations of biological databases, but most of this effort has gone to generalized systems that are not particularly appropriate for the problems faced by diatomists.

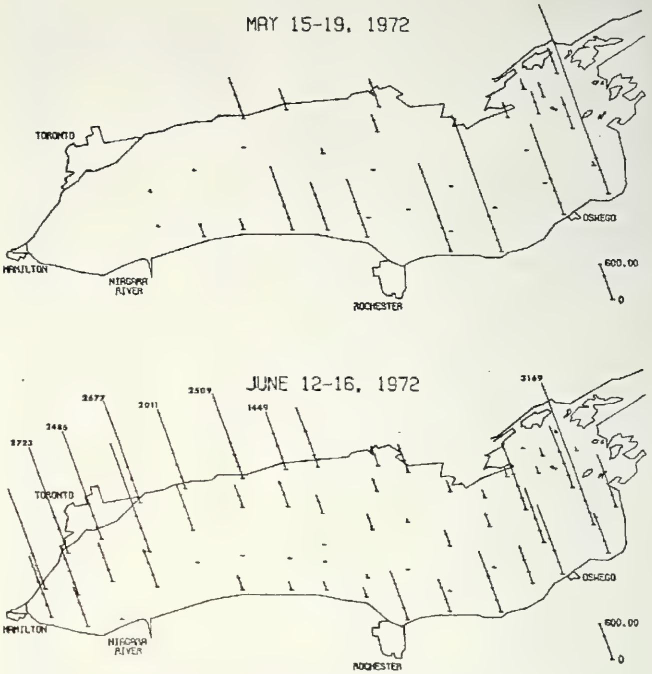

FIGURE 7. Example of species data plotted from a similar study. Distribution of *S. binderanus* in Lake Ontario in the spring of 1972. In the lower image, actual numerical values are given at the top of bars when values are too large to conveniently plot at scale used (from Stoermer et al. 1974).

Part of the problem is the structure and economics of the computer industry. The very rapid expansion of computing power (Moore's Law) causes rapid obsolescence in microcomputers, a trend that the industry has capitalized on. It must also be said that University administrations, at least in this country, have been alert to the fact that the cost of centralized mainframe computer systems usually becomes their responsibility, whereas much of the cost of decentralized systems falls on Departments, or individual investigators. It is also a truism that the quickest way for a software company to go broke is to design a perfect product. It is economically much more rewarding to design something marginally adequate that can continue to be upgraded. All of this militates against development of a stable continuing system, and makes upgrading of a developed system very difficult, in that most resources are devoted to exploiting "exciting" new technologies, rather than adapting existing databases to them as they arise.

In the case of our system described above, we eventually became victims of the technology transition. FIDO was much more complete and easy to use than any of the early microcomputer database programs, and we continued to use it well past the transition from mainframe-based to a microcomputer-based network system. We were unable to obtain support for conversion from either local or national funding sources, so much of the data accumulated during this era exists only on hardcopy and tapes that are rapidly becoming unreadable. Part of the reason for this was that we were somewhat too clever in using "latest technologies" of the day that were specific to the University of Michigan mainframe computer system.

Perhaps the "take home" message for independent laboratories is to develop and use the simplest system adequate to your specific needs, and upgrade and maintain it judiciously. Although the latest and greatest in technology is always attractive, pioneers in technology areas often suffer different, but equally painful, slings and arrows as did the geographic pioneers of past centuries. In this regard, I think the "open software" movement offers great promise.

PRESENT AND FUTURE CONSIDERATIONS

And I continue to feel that computer assisted approaches offer the best avenue for "marrying" the needs of taxonomists and ecologists. As I have discussed elsewhere (Stoermer 2001) it is foolish for ecologists to expect taxonomic treatises on diatoms of the type generally available for "higher" organisms to become available in the foreseeable future. This being the case, it is really necessary to incorporate good taxonomic practice into routine analytical work and assure that project outputs are useful to people whose primary interests are in taxonomy and systematics. At the same time, it behooves the few people in the latter category to be more proactive in addressing the resources potentially available from ecological studies.

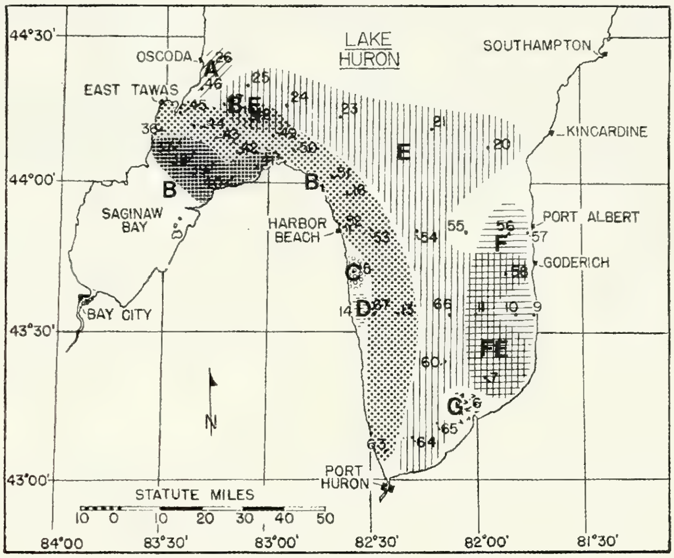

FIGURE 8. Representation of phytoplankton community structure in southern Lake Huron based on samples taken 4-8 June 1974 under west wind forcing. Associations were determined using dimensional ordination and principal components analysis (from Stoermer and Kreis 1980). Materials and phytoplankton from badly polluted Saginaw Bay are entrained by the spring thermal bar and, combined with other local shoreline sources, generate "eutrophic" associations in the western portion of the lake. Mostly agricultural and minor industrial sources from the Canadian shore, also entrained by the spring thermal bar, produce more "mesotrophic" associations in the eastern portion of the lake. The oligotrophic associations expected in a large lake of this type are only found in the offshore waters.

At present, it is quite feasible for workstations used in diatom analysis to capture and maintain not only the analysts' taxonomic decisions, but also images of exemplar specimens such decisions are based on, the pertinent locality information, and the precise location on a slide of each specimen assigned to a given category. At the same time, the analyst should be able to address taxonomic information and identification aids, such as image analysis, directly and in real time.

Whereas the digital tools now available offer exciting possibilities, they also present some real challenges and dangers. The possibilities for enhanced data display and sharing make the possibility of "consensus floras" more attractive. Although this may be useful, and indeed necessary, in the context of a particular ecological project, such efforts can easily degenerate into lowest common denominator solutions that actually retard scientific progress in the general field, rather than advancing it. Diatomists are in a particularly difficult situation in this regard. Taxonomic information in our field is virtually exploding, but most funding agencies, both those traditionally supporting ecological research and those supporting taxonomic tend to take large organisms as their model for understanding diversity. Even at this level, there is no logical expectation of ever establishing a truly "stable" taxonomic system unless we are willing to freeze knowledge in some imperfect state. In the case of diatoms, the present state is grossly imperfect and the expectation of stability is demonstrably unscientific. Given that there are snares and pitfalls to be avoided, currently available technologies offer those bold and resourceful enough to utilize them great possibilities. These range from purely exploratory — we are still in the era where simple discovery and description probably advances the field more than any other approach — to application and incorporation of available tools for taxonomic and ecological questions.

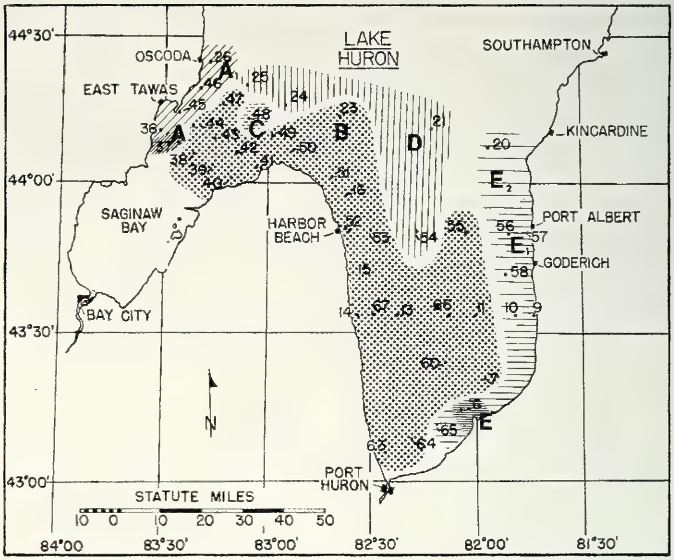

FIGURE 9. Representation of phytoplankton associations from the same study shown in Figure 8. In this case, data were collected 26-31 August under east wind forcing. A large upwelling has occurred in the eastern region of the lake. This combined with local shoreline sources results in atypical phytoplankton associations in the eastern nearshore region. The extent of nutrient re-supply also causes somewhat atypical summer associations in most of the southern portion of the lake, and these communities intrude into Saginaw Bay, as the expected eutrophic communities are transported northward along the Michigan (western) shore. The expected offshore "oligotrophic" summer phytoplankton association is only found at a few stations in the north-central quarter.

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Taxonomy and Ecology: An Inseparable Pair

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Some examples from the diatom genera *Gyrosigma* and *Pleurosigma* are presented to illustrate the following postulates: (1)the notion that taxonomy is an "old-fashioned" activity is a relict of the pseudo-progessive Seventies; (2) faulty taxonomy results in irreproducible pseudo-science, e.g., in unverifiable ecological conclusions; (3) ecological studies on diatoms should take account of the micro-sized biotope in which diatoms live and of the time factor; (4) phenotypically identical populations in widely different habitats may constitute different "ecospecies."

The central theme of this workshop is the synergy between taxonomy and ecology in the study of diatoms and the application of its results. To set the stage, I will try to illustrate what may happen if this synergy is disregarded with some examples from the genera *Gyrosigma* and *Pleurosigma* — not because they are particularly important in this respect, but as a result of personal interest. Call it a "travelogue" in which we travel from one taxon to another and from one issue to the next. In addition, I will offer some personal comments on the financial, political and societal context in which we have to study diatoms.

THE TAXONOMIC SITUATION

In many countries including The Netherlands, the situation for diatom taxonomy is deplorable. No specific budgets are available and expertise in the practical application of diatom taxonomy is at risk of being destroyed by budget cuts that may lead to the closure of entire departments.

This is partly due to the fact that funding for basic research is becoming difficult to secure, because research may be at the mercy of leaders who think that Science can be profit-driven. But another factor involved is the widespread image of taxonomy as an unimportant activity, and this is a serious problem we must address.

The Image of Taxonomy

In the first place, the very nature of taxonomy is often unclear, even to some diatomists. Students think that the short courses they receive in identification of the more common diatoms constitute "taxonomy." Taxonomy, however, is the fundamental investigation of organisms aiming at a circumscription of their biological (that is, genetic) individuality.

Secondly, in some circles there is a strong aversion to what they *think* is "diatom taxonomy" because in their past experience this has resulted in long lists of names permitting no scientific conclusion whatsoever. A floristic inventory does not equate to taxonomy and it's the diatomists' own fault that this antipathy has arisen.

Thirdly, there is the widespread misconception that taxonomy consists of the description of new species or varieties. The realisation that taxonomy may instead have to start with the *elimination* of established but invalid "pseudospecies" may come as a surprise to workers not specialising in the subject.

Finally, the practice of taxonomy, with its careful procedure of literature research, tracing herbarium materials, determining synonyms and formal typification is dismissed as "old-fashioned" by some. Many biologists are unaware that the only permissible taxonomic procedure for diatoms (as for other algal groups and higher plants) must follow the rules of the ICBN (International Code of Botanical Nomenclature).

In this situation we must formulate convincing reasons why diatom studies involving taxonomy are important and should be supported. Unfortunately, the principal character separating humans from other animals — the Pursuit of Knowledge — is no longer regarded as sufficient *per se* by potential funders. Therefore, our arguments should in a sense also be "politically correct," fitting in with the societal-political issues of the moment. This may seem a mercenary attitude, but it merely recognises the reality that science is pursued in a societal — and thus political — context.

Taxonomy and Ecology: Inseparable

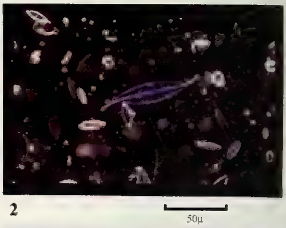
The examples given here relate to the diatom genera *Gyrosigma* and *Pleurosigma*. These diatoms illustrate the lack of taxonomic research very well, as evidenced by the amazing fact that of the many thousands of diatom illustrations published in the course of 85 years in Schmidt's *Atlas* (1875–1959) *not a single one* showed a representative of these genera!

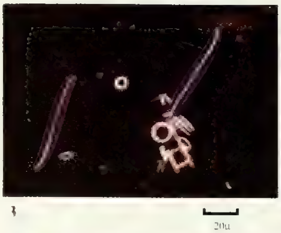
Neglect of taxonomy violates the most basic rule of science. For human communication of *any* nature to make any sense at all, the entities under discussion must be unambiguously defined. If no proper taxonomic separation were made between *Canis lupus* and *Canis domesticus*, one would conclude that the development of human society since the Neolithic has been associated with an explosive increase in the population of wolves.

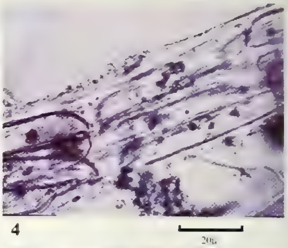
Only when the identity of an organism has been unambiguously fixed does it become possible to determine its biological characteristics: its physiology, nutritional requirements, habitat and biogeography. Only when these are known, the organism can become a source of information on the Earth's history. This is especially the case for diatoms, whose siliceous exoskeleton is both taxonomically informative and durable, permitting conclusions over many millions of years.

Example (Fig. 1): Published studies on the Dutch Wadden have described an abundant presence of *Gyrosigma spenceri* (Quekett) Griffith et Henfrey. The type material of this diatom indicates a freshwater environment, however. This would imply that either the Dutch Wadden Sea is subject to massive freshwater influx (which is not the case) or that *Gyrosigma spenceri* has an ecology ranging from freshwater to fully marine. Taxonomic studies have shown, however, that *Gyrosigma spenceri* — for 150 years one of the most frequently recorded members of the genus — is merely a later name for *Gyrosigma acuminatum* (Kützing) Rabenhorst, a purely freshwater diatom. In addition, it became clear that at least 6 different species with different ecologies ranging from freshwater to brackish and fully marine have been called "*Gyrosigma spenceri*," or varieties thereof. The previous studies thus presented irreproducible results because of taxonomic errors (Sterrenburg 1995, 1997; Sterrenburg and Underwood 1997).

The taxonomy of *Gyrosigma* and *Pleurosigma* species is a challenge, but their ecology is not particularly diverse. The freshwater species all avoid acidic, oligotrophic waters but do not appear to permit fine ecological distinctions. Also, especially in Holland there are major gradients in salinity from freshwater via brackish to fully marine and these show that some *Gyrosigma* and a few *Pleurosigma* species can tolerate a wide range of salinity. The genera clearly flourish best in the marine littoral and in general they favour the presence of organic detritus, but for really sensitive ecological indicators other diatom genera offer better candidates.







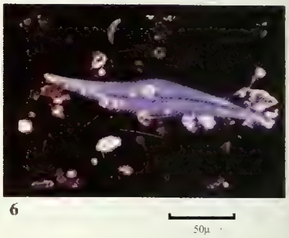


FIGURE 1. Specimen typical of "*Gyrosigma spenceri*" identifications in the literature: *G. acuminatum* from a ±freshwater ditch, North Holland. Bar = 50 µm.

FIGURE 2. *Gyrosigma wormleyi*, Salton Sea, California, USA. Morphologically this is a complete match for the freshwater type specimens. Bar = 50 µm.

FIGURE 3. Specimens matching the protologue of *Gyrosigma exilis* from the only population observed so far in The Netherlands (North Holland). Bar = 20 µm.

FIGURE 4. Live specimens of *Gyrosigma obliquum* in mucus tubes. Samoa, Pacific. Bar = 20 µm.

FIGURE 5. *Gyrosigma spectabile* from one of the "standing crops" in the Florianopolis area, Brazil. Bar = 50 µm.

FIGURE 6. Specimen fully matching the New Zealand type specimens of *Pleurosigma sterrenburgii*, from one of the rich populations seen in the Jadebusen, North Germany. Bar = 50 µm.

EXAMPLE (FIG. 2): The most extreme case so far observed is *G. wormleyi* (Sullivant) Boyer, also on record as the illegitimate synonym *G. parkeri* (Harrison) Elmore. Its type material is definitely freshwater and I have indeed collected it in non-saline Dutch waters, but I have also found flourishing populations in the marine littoral of Cameroon, for instance. Also, Tiffany and I have verified that it grows abundantly in the Salton Sea, California, which is 30% saltier than seawater! Morphologically, the marine and the Salton Sea populations are completely identical to the freshwater type specimens so that identifications arrive at the same morphospecies. One could think of two different explanations: (1) *G. wormleyi* is very euryhaline by nature, any population being able to grow under widely different conditions of salinity; or (2) The populations from highly saline waters observed might not be genetically compatible with the type. The latter might apply to the Salton Sea populations in particular, because the Salton Sea is man-made and the result of an engineering mishap about a century ago. This caused the Colorado River to be dumped into a natural depression in the Californian desert and as the salinity of this artificial lake increased over time, an originally "freshwater population" from the Colorado River may have adapted and drifted apart genetically. One would need to verify whether these individuals can still cross with their parent line — if not, they should be considered a different "ecospecies."

This shows that we may need to consider the species concept from the ecological as well as the traditional taxonomic perspectives (see Sterrenburg 1994; Sterrenburg, Tiffany, and Lange 2000).

Spatial and Temporal Factors

Examination of the literature of freshwater diatom surveys that include ecological data raises the question how reliable such "traditional" data really are. Typical sampling methods comprise too broad a scale for microscopic, rapidly dividing organisms such as diatoms, both spatially and temporally. Scaling down could reveal much more about the taxonomy and ecology of diatoms.

Suppose that physico-chemical analysis of a water column sample from a stagnant freshwater pool yields a certain pH and certain values for salinity, phosphate etc. Certainly, these values do not define the ecology of the bottom-dwelling as well as the epiphytic and planktonic species. Such a stagnant pool — because of the absence of mixing — shows a series of gradients in temperature, insolation, pH, mineral concentrations and organic compounds that may favour or inhibit the growth of certain species. When organic matter in the mud decays, this will lead to strong local physico-chemical gradients, which could lead to major changes in the diatom assemblage over very short distances. For micro-organisms we would need to scale down properly, using microsensing instead of analysing "a bulk water column sample."

EXAMPLE: (FIG. 3): This small freshwater *Gyrosigma* matches the protologue for *G. exilis* Grunow. It had never been described for The Netherlands and the only locality where I have found it is a spot measuring only a few square meters: a sandy slope wetted by a trickle of freshwater in a reclaimed area called the Wieringermeer in the province of North Holland. In this tiny area, I have found that the species has continued to grow for about 20 years. Topological isolation is not involved, the physico-chemical conditions appear to be the same as everywhere else in the area and although some ecological factor is likely to be involved, I can offer no explanation.

For intertidal mudflats in the marine littoral, one does not expect to find major local ecological differences over short distances as intensive mixing is involved, but the time factor also needs to be considered.

EXAMPLE: (FIG. 4): When this sample was collected from an intertidal mudflat on the coast of West Samoa, the temperature of the surface mud was near 50°C and evaporation had led to the appearance of salt crusts in some places — indicating a hypersaline habitat. A few minutes later, a torrential monsoon rain submerged the site ankle-deep in cool and only mildly brackish water. The diatom flora here has to be resistant against severe osmotic shock and probably for protection, *Gyrosigma obliquum* Grunow (like several other diatoms from such habitats) can develop thick mucus tubes. An ecological "snapshot" of the habitat may therefore be insufficient, one must consider the ecological extremes to which the diatom may be exposed during its lifetime (Sterrenburg 1989).

In other words, we may have to look at diatom ecology at the proper spatial and temporal scales. Such an integration of ecology and taxonomy could certainly yield valuable data from the purely scientific point of view, but I am not sure we could convince many politicians to finance it.

The Environment

Studies on the impact of human acitivites on the environment are certainly regarded as "politically correct." A previous generation of engineers and scientists was able to pursue a career studying acid rain and its effects. For this subject, diatoms have indeed contributed valuable data — provided there was a sound taxonomic basis for identification of species tolerant to low pH. But because electricity generation is now much cleaner, acid rain as a source of money has dried up in the developed countries.

Global warming was another good source of potential income for research but it may not be easy to find strong arguments for improved diatom taxonomy in support of short-term global warming studies — in contrast to long-term paleoclimatology, of course. And because of the recent political dissent over the Kyoto protocol, the immediate future for global warming studies looks somewhat chilly anyway in certain countries.

Water quality studies continue to be a modest but steady source of income for some diatomists, but it may not be easy to convince our paying customers of the necessity of further development of taxonomy here. Usually, customers want to hear simple and unambiguous answers to their questions. Customer relations would not receive a major boost if we told them that we'd have to spend lots of extra time and money to answer their question because we're not really sure our taxonomy is correct! Scientifically, this may be quite true, but we'd eliminate ourselves from the market.

BIODIVERSITY

The situation becomes different, however, if we consider taxonomy and ecology in relation to studies on biodiversity. And "biodiversity" *has* become a word even government circles have become familiar with. It is certainly politically correct to express concern about the extinction of species due to human impact. Therefore, a taxonomically impeccable record of verified distribution patterns is highly valuable. The basic shortcoming in the concern about the loss of species diversity expressed by non-scientists is that we *should first know what there is in an area before we can determine what we are losing* — and that is far from being the case.

If we take the marine littoral as an example, a survey of the literature will immediately show that data on the diatom species diversity of many areas of the globe may amount to a single publication based on one or two poorly documented samples collected in the 19th century. This is especially true for tropical coasts, and there the situation is particularly serious for three reasons:

(1) these may be the areas where species diversity in certain diatom genera may be *particularly high*;
(2) they may be under severe human-related ecological pressure — for instance, the large-scale destruction of coastal wetlands and mangrove forests, or pollution by industrial effluents or sewage;
(3) but tropical and subtropical countries are often precisely the areas where funding for research is *minimal*!

EXAMPLE: (FIG. 5): The total verifiable documentation of *G. spectabile* Grunow ex Peragallo consisted of a schematic drawing of a single specimen and minimal diagnosis published in 1891. De Souza-Mosimann, Fernandes, and I have verified that this presumably "rare and obscure" species, which had not been recorded for over a century, is actually an abundant member of the standing diatom crop of the coast of South Brazil to French Guyana (see Sterrenburg, de Souza-Mosimann, and Fernandes 2002)!

But even for our own backyard, great improvement in diatom biodiversity data is possible — and necessary before we can draw useful conclusions.

EXAMPLE: (FIG. 6): Ten years ago, Stidolph described this diatom as a new species from New Zealand. I had never found it in samples from any other area, e.g., the Indian Ocean, Pacific, Caribbean, Arabian Gulf or Mediterranean until a few months ago when I found large populations in the German Jadebusen! This second, literally antipodal, record of *Pleurosigma sterrenburgii* Stidolph constitutes the greatest extension of biogeography possible, and, since then, it has been observed in large numbers in that area (Witkowski, pers. commun.; Stidolph 1993).

To illustrate the actual species diversity in *Gyrosigma* and *Pleurosigma* for The Netherlands: the Dutch flora of Van der Werff and Huls recorded about a dozen taxa for these genera. About half of these are synonyms or confused entities, so there remained only about half a dozen Dutch sigmoid diatoms whose identity was reasonably certain. So far, I have recorded about 60 species from these genera in the same area — and more continue to be found. With a Macchiavellian line of reasoning, it could be claimed that human activity does not harm Nature at all but can instead lead to a *ten-fold increase in species diversity.*

Although a combination of taxonomy and ecology properly scaled in space and time would be ideal, even a more modest effort to get an insight into the huge diversity of diatoms, with *verified* data on their biogeography and reliable information on their autecology, is necessary and can be argued to be compatible with the current societal-political trends. It can contribute to the challenge raised by the All Species Foundation (*www.all-species.org*) to catalogue all the World's living beings!

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Microalgal (Microphytobenthic) Biofilms in Shallow Coastal Waters: How Important are Species?

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Microphytobenthic biofilms, dominated by diatoms, are important components in many intertidal and shallow water marine environments. Much of our understanding of their functioning comes from studies that have not treated species composition as a significant factor. Conversely, many studies concerned with species distribution have not encompassed our understanding of the dynamic nature of biofilms. This paper presents data to show there are significant differences in the behaviour and physiology of different taxa of diatoms within the same biofilm, and that species respond differently to the external nutrient environment. These data indicate that consideration of the importance of the species-niche (both autecological and synecological) can be beneficial to both taxonomy and ecology.

In many marine and estuarine environments, large areas of shallow intertidal and subtidal habitats are dominated by microalgal assemblages. These are known by a number of terms, epipsammon, epipelon, periphyton, benthic microalgae and microphytobenthos (Round et al. 1990). Although these communities are mixed assemblages containing representatives of many algal groups, those communities found on muddy, and to some extent, sandy sediments are dominated by diatoms (Admiraal 1984; Underwood and Kromkamp 1999). Overall species richness of marine benthic diatoms is quite high, particularly over geographical scales (Witkowski et al. 2000), yet within a particular environment, it is more usual to find only a few (20+) taxa that are numerically dominate within assemblages (Admiraal and Peletier 1980; Colijn and Dijkema 1981; Underwood 1994; Thornton et al. 2002).

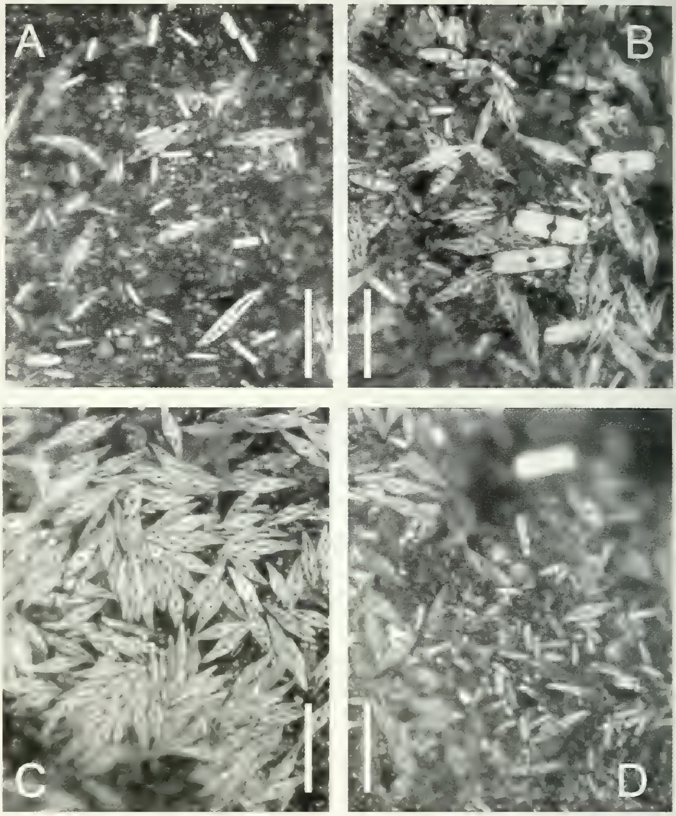
The ecology of these systems has been extensively studied, in particular estuarine intertidal habitats, saltmarshes and in shallow coastal seas, primarily the Baltic. From these studies we know that in ecological terms, microphytobenthic biofilms are extremely important in ecosystem functioning. The primary production of microphytobenthos can be very high, and this can contribute a significant proportion of the autochthonous carbon production in estuarine and shallow lagoon environments (Underwood and Kromkamp 1999; Cahoon 1999). Microphytobenthos also mediate a whole range of biogeochemical processes, such as nutrient exchange and nitrogen cycling and attenuation of nitrogen loads (Dong et al. 2000; Thornton et al. 2002). This is because biofilms occur at the interface between the water column and the sediment, and within the relatively narrow zone, high rates of biological activity can result in oxygen supersaturation, release of organic carbon exudates, anaerobic conditions and rapidly changing chemical gradients (Underwood and Kromkamp 1999). Microphytobenthos can sequester phosphorous, silicates and nitrogen from the water column and both enhance, and inhibit, denitrification and coupled nitrification-denitrification (Sundbäck et al. 1991; Rysgaard et al. 1994; Dong et al. 2000). As such, extensive areas of biofilms can significantly attenuate the flux of nutrients through coastal areas (Thornton et al. 2002). Another property of biofilms is their ability to increase the stability of sediments, usually through the production of mucilage (extracellular polymeric substances, EPS) (Smith and Underwood 1998, 2000; de Brouwer and Stal 2001), which acts to increase the critical erosion stress required to initiate erosion of flocs from the sediment bed (Widdows et al. 2000; Tolhurst et al. 1999; Underwood and Paterson 2003). Thus biofilm-inhabited sediments are more difficult to erode, and biofilm-inhabited sediments more rapidly trap and hold, fine sediments (Underwood and Paterson 1993, 2003).

As this brief overview makes clear, diatom-rich biofilms play a very important role in the ecology of shallow-water systems. However, a study of the literature clearly shows that functional studies on biofilms predominantly ignore species composition, and treat the assemblage as a black box — "a biofilm." Conversely papers dealing with species distribution tend to rely on a very descriptive approach to defining the environment, usually in terms of nutrient concentrations, salinity and temperature. These latter (state) variables tend to be taken as a valid description of the potential niche of a species, without regard to the changeable nature of these variables over short term (hours - fluxes of nutrients rather than concentrations, diel fluctuations in temperature) and medium term (days — changes in tidal exposure period, meteorological conditions) time scales.

Can knowledge about the species of diatoms in a biofilm improve on our understanding of biofilm processes? Why should functional ecologists be interested in species composition, and therefore by association, require a good and robust taxonomy? This paper aims to show that, at least in two areas, photosynthesis and response to nutrients, species-information can improve our understanding of biofilm function.

PHOTOSYNTHESIS AND DIFFERENCES BETWEEN BIOFILMS

In general, it has been shown that light intensity influences the rate of photosynthesis and overall primary production of biofilms (Underwood and Kromkamp 1999). This reasoning underlies many models that predict benthic primary production on the basis of irradiance data and biomass (Serôdio and Catarino 2000). However, this view is currently being reassessed. This is partly because some studies are based on using slurry systems for measuring photosynthesis. Using a slurry (a mixture of biofilm and sediment) removes the 3D structure of the biofilm and prevents cells from following their natural migration patterns. Placing cells in suspension means that they behave like phytoplankton and respond to light accordingly (Underwood and Kromkamp 1999). Recent developments in imaging technology have now made it possible to measure the photosynthetic performance of different cells within intact biofilms (Oxborough et al. 2000). In the natural environment, microphytobenthos show complex behaviours in response to light. In a study of microphytobenthos in the Tagus estuary, Perkins et al. (2001) showed that during tidal exposure when light levels are low, cells accumulate at the surface, but migrate away from the surface at high irradiances. This was described as a type of behavioural photoacclimation. In the Tagus estuary (Miles and Sundbäck 2000; Perkins et al. 2001), and Colne estuary (Perkins et al., unpublished data), this can result in highest rates of photosynthesis early in the morning, despite light levels increasing towards midday, as cells position themselves in an optimum light climate within the biofilm. These movements can be very rapid, and the surface community can change from a biofilm dominated by diatoms to one dominated by euglenoid algae in 10 minutes as light intensity increases (Perkins et al. 2002). Similar patterns of migration and migration responses of different microphytobenthos have been shown using low temperature electron microscopy coupled with measurements of spectral reflectance off mudflats (Paterson et al. 1998). Such micro-migrations are superimposed over the tidal migration of cells to and from the sediments surface. Fig. 1A–D shows the change in species composition at the same point on the surface of a biofilm over a diel exposure period. Substantial changes in species composition are evident, so that measurements over a period of time will be measuring the photosynthesis of different populations of diatoms. Imaging has revealed that individual taxa can have significantly different photosynthetic efficiencies (the rate at which captured light energy is converted to electrons and using in photosynthesis). Oxborough et al. 2000 showed that the photosynthetic efficiency of three diatom species (*Pleurosigma angulatum* (Quekett) W. Sm., *Gyrosigma littorale* (W. Sm.) Griffith et Henfrey and *Plagiotropis vitrea* (W. Sm.) Kuntze differed from each other at lower light intensities, and all three species were significantly less efficient than *Euglena* sp. at higher irradiances (> 500 µmol m^{-2} s^{-1}). Differences between species also appear during tidal exposure cycles. Fig. 2A shows the composition of a surface biofilm during a diel exposure period. Three diatom taxa dominated this particular biofilm (*P. angulatum*, *P. vitrea* and *Nitzschia dubia* W. Sm.), with small *Nitzschia* spp becoming abundant at the end of the tidal period. At the beginning of the day, the three diatom taxa had the same photosynthetic efficiency, but by midday, all three taxa showed reduced efficiencies, but also that there were significant differences in photosynthetic efficiency between species (Fig. 2B). These differences will combine to produce overall biofilm functioning, and may even be selective for particular species under different conditions. These hypotheses need to be tested, but it is evident from these data that all cells within a biofilm do not behave the same. Thus ecological function is a property that requires knowledge of species composition (including good taxonomic resolution).



FIGURES 1A–D. Temporal changes in the surface composition of a microphytobenthic biofilm from the Colne estuary, UK, over a tidal exposure period taken using a microscope-based, fluorescence imaging system (Oxborough *et al.* 2000). All images are of the same area at (A) 07.30 h, (B) 11.00 h, (C) 15.30 h, (D) 18.00 h. Scale bar = 200 µm.

This requirement to incorporate species and assemblage information with measures of community functioning is clearly shown in a study of tropical microphytobenthos. Measurements of photosynthetic efficiency, characterisation of the light climate within the sediments, algal biomass and maximum rates of relative electron transport (a proxy measure for photosynthesis) were found to be significantly different between microphytobenthos from different habitats (Underwood 2002). The conventional explanation (in the absence of any species composition information)

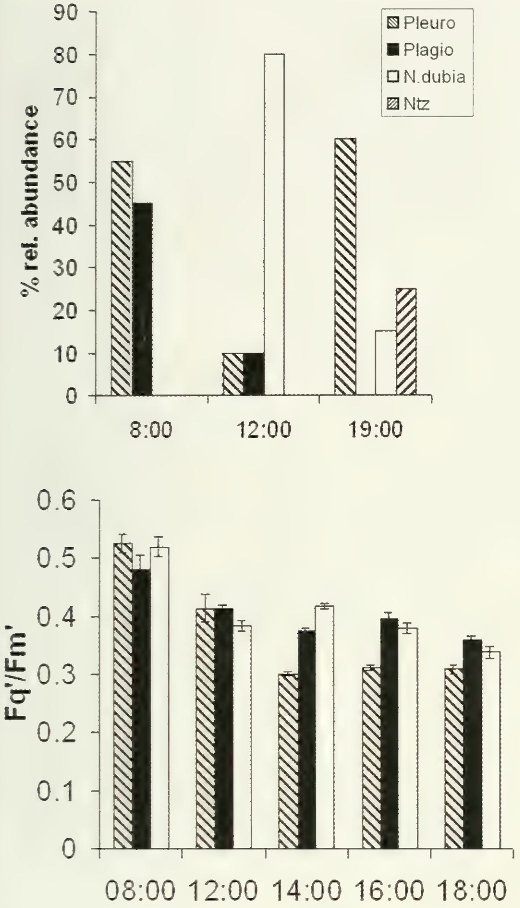


FIGURE 2. (A). Relative abundance (%) of 4 taxa of benthic diatom present at the surface of a biofilm at 3 periods over a diel cycle. (B) Measures of individual cell photosynthetic efficiency (*Fq' / Fm'*) showing significant differences between taxa during the later part of the diel period. Values means ± SE, n = 10 or greater.

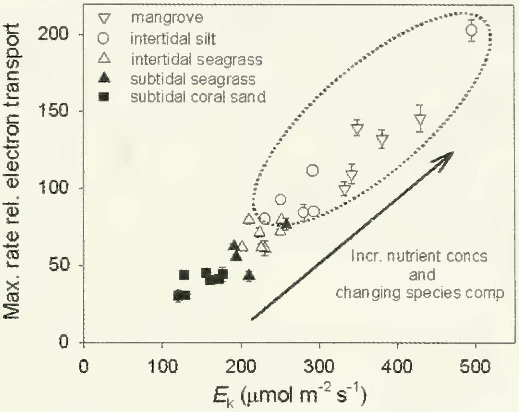


FIGURE 3. Relationships between the maximum relative electron transport rate and the light saturation parameter E_k for microphytobenthic biofilms from 5 different tropical marine habitats, showing the significant correlation with nutrients, but also changing species composition and the occurrence of vertical migration within particular biofilms (dotted ellipse). (Redrawn from Underwood 2002).

would be to explain the significant correlations between maximum rates of relative electron transport (a proxy measure for photosynthesis) and E_k (the half light saturation coefficient) with nutrient concentrations in terms of nutrient limitation causing biofilms to be less efficient. However, this significant "nutrient photosynthesis" relationship also corresponded directly with differences in species composition between biofilms (Fig. 3). Biofilms showing the highest values of photosynthetic parameters also exhibited strong vertical migration in response to light and comprised many large, motile taxa, such as *Hantzschia virgata* (Roper) Grun., *Berkeleya scopolurum* (Bréb.) Cox and *Navicula* species. The shallow subtidal biofilms in the coral sands and seagrasses had a different flora, dominated by *Diploneis*, *Amphora*, *Psammodictyon*, *Tryblionella* and *Mastogloia* and showed little evidence of vertical migration in response to light stress or tidal rhythms. Thus the differences in biofilm function can also be mapped onto differences in species composition as well as the more conventional explanations of nutrient limitation or photoacclimation.

SPECIES AS NUTRIENT INDICATORS

There are increasing data to support the hypothesis that microphytobenthos can be used as indicators of environmental conditions, particularly nutrient concentrations and salinity. This is leading to the development of trophic indices for marine and estuarine systems similar to those currently available for freshwaters. The estuarine environment is a particular challenge in this respect, partly because of the significant human impacts on estuarine habitats, due to proximity of large centres of human habitation and industry (Hessen 1999; Nedwell et al. 1999), but also because of the wide range of conditions estuarine taxa have to tolerate. Thus estuarine microphytobenthos appear to be tolerant of a fluctuating range of conditions (Admiraal 1984). In the Baltic Sea, various diatom taxa have been shown to be sensitive to the well-defined and constant salinity gradient present in the Baltic Sea (Snoeijs 1993; Snoeijs and Vilbaste 1994;Snoeijs and Potopova 1995; Snoeijs and Kasperovièiene 1996; Snoeijs and Balashova 1998). This stable gradient may allow quite narrow species niches to be defined, but it would be incorrect to attribute the same salinity niche to one of these taxa if it was found in a meso- or macrotidal estuarine environment. However, even in the more variable environment of tidal estuaries, species shifts with nutrients can be demonstrated. A number of field studies, long-term data sets, experimental-nutrient enrichments, experimental studies in mesocosms and on isolated cultures have all indicated that some taxa (e.g., *Fallacia pygmaea*, *Navicula salinarum*) have greater tolerance to high nutrient concentrations and organic loads and may potentially be indicators (Sullivan 1976, 1981; Admiraal 1984; Peletier 1996; Underwood et al. 1998; Sullivan 1999). It is clear that broad scale patterns of species variability reflect changed environmental conditions (sediment type, water flow, salinity). However, more detailed studies are needed to demonstrate that the diatom community at a particular site will change if nutrient loads increase or decrease (Peletier 1996). In particular, experimental testing of hypotheses derived from correlative field measurements of species occurrence and environmental variables, to demonstrate causes and mechanisms for changing species composition is needed. For example, Figure 4 shows the maximum intrinsic growth rate (μ d^{-1}) of cultures of *Navicula phyllepta* Kützing isolated from the Colne estuary, U.K. and grown in a range of nitrogen con-

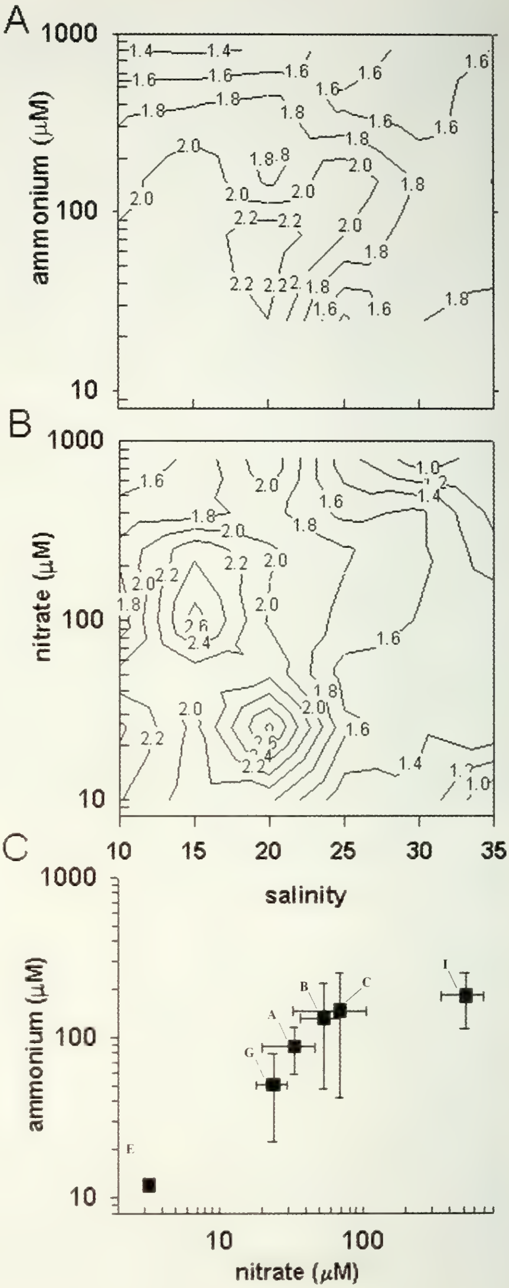


FIGURE 4. Maximum intrinsic growth rates (μ d^{-1}) of *Navicula phyllepta* grown in culture in a range of ammonium and salinity (4A) or nitrate and salinity (4B) conditions. (4C) Occurrence of various diatom assemblages related to ammonium and nitrate concentrations over a 12 month period in the Colne estuary, UK. Assemblages A, B and C were dominated by *N. phyllepta.* (Redrawn from Underwood and Provot 2000 and Thornton et al. 2002.)

centrations (ammonium and nitrate) at different salinities. *Navicula phyllepta* showed maximum growth within an inorganic nitrogen range of between 50–300 µM and at salinities between 15–25 ppt (Fig 4A, 4B). These culture data agree closely with field data, where assemblages dominated by *N. phyllepta* were present in the estuary when nitrate and ammonium concentrations were within this range (Fig 4C). Underwood and Provot (2000) showed that three taxa of *Navicula* had different, but overlapping nitrogen and salinity optima, and these may be partly an explanation for field patterns. Such experimental approaches do need to consider the physiological responses of cells to changing environments, particularly the ability of cells to adapt to changing conditions.

CONCLUSIONS

There are good reasons to encourage a "marriage" of taxonomy with ecology. For the reasons outlined above, the ecological importance of biofilms has meant that substantial funding has been provided for scientific investigations of biofilm functioning in the marine environment. Such studies have been quick to embrace new technologies to increase the resolution of measurement down to the microscale and now it is possible to measure and visualise the environment at a scale comparable with that of individual diatom cells. This provides a great opportunity to link ecosystem functioning with knowledge of individual species. Up till now, much of this ecological research has tended to ignore species composition as a factor in biofilm functioning. New techniques, such as *in situ* quantitative PCR and using fluorescently-labelled markers to identify species, provide a mechanism for taxonomic expertise to interface with functional studies. This does require diatom taxonomy to broaden its view on what characteristics of diatoms are important taxonomically and a willingness to "widen" the species concept away from the rigid morphological definition of a species. The "marriage" will be harmonious when separations of species on taxonomic grounds are found to match, in some way, the functioning of those taxa in the environment. There is plenty of scope within the marine microphytobenthos to investigate the concept of the species-niche in its broadest sense (both autecological and synecological) and to use this information in both taxonomy and ecology.

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Structural, Biochemical and Molecular Investigations on Wadden Sea Diatoms: Field Studies and Laboratory Experiments

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WADDEN SEA-INHABITING DIATOMS

Wadden Sea sediments are inhabited mainly by diatoms, euglenoids and cyanobacteria. Diatoms may dominate these habitats with respect to species diversity and cell density and often exceed cell numbers of more than 10^6 per cm^2 sediment. Several sediment-inhabiting diatom species show a rhythmic vertical migration (VM) behaviour and move up onto the surface when the water drains off and down into the sediment bed with the incoming tide (Harper 1969, 1976; Happey-Wood and Jones 1988; Hopkins 1966; Palmer and Round 1965; Round and Happey 1965; Round and Eaton 1966). They, thus, have to face dramatic changes of several physical and chemical parameters in their natural habitat: tidal inundation results in reduced concentrations of gases and lowered light intensities, but gives rise to almost constant values of temperature, salinity, pH and nutrients. During tidal emersion these parameters may vary drastically: salinity and temperature may increase and lead to desiccation and temperature stresses, respectively, whereas light intensities of up to 2000 μmol photons m^{-2} s^{-1} may cause photoinhibition (Underwood 2002). The dramatic changes will have a great impact on the community structure on a long-term scale (months and years) and, on a short time scale (minutes and hours), will result in adaptation processes within the cells. For investigating both kind of responses, temporal changes in community structure and short-term cellular adaptation processes, it is necessary to use "old-fashioned" classical methods of diatom research and "modern," i.e., molecular, biophysical, and biochemical methods in parallel. In the following sections, we give a short summary of the methods used in our lab to study Wadden Sea diatoms. The methodological approaches have now been well established for laboratory experiments, and it is a challenge to transfer and use this repertoire of methods directly in the field or on field samples.

CLASSICAL TAXONOMY AND IDENTIFICATION OF WADDEN SEA-INHABITING DIATOMS

To study long-term changes of the diatom community the use of classical methods for diatom identification are indispensable. Usually, acid-cleaned diatom frustules are used for this purpose. Wadden Sea sediment samples collected at regular intervals over periods of several months or even

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years from the same sampling area can be easily treated with HCl and H_2O_2 as oxidative agents followed each by repetitive washing steps with water. Light microscopy and scanning electron microscopy give information on species diversity and species abundances. These data allow statements on local and temporal successions of distinct species at a given habitat. A major disadvantage of this approach is that no information on the distribution of individual cells within the sediment bed becomes available. For this, sediment cores have to be withdrawn, frozen and sectioned horizontally into slices of 200 to 500 μm width (de Brouwer and Stal 2001; Kelly et al. 2001). The slices can also be used for frustule preparations.

LABORATORY TIDAL MICRO-ECOSYSTEM AND MINI-MESOCOSMS

Vertical movement can be investigated in the laboratory under almost natural conditions. Sediment samples collected in the field and transferred to the laboratory do not show fluctuations in species abundance during the first two weeks after transfer (Defew et al. 2002). During this time period, tidal immersion and tidal emersion can be simulated in tidal micro-ecosystems (Paterson 1986). Alternatively, sediment samples can be put into mini-mesocosms, i.e., aluminium stubs (Fig. 1) or small petri dishes, which are placed in wet chambers and subjected to defined regimes of several physical and chemical parameters: light intensity, light quality, temperature, pH, salinity, or gas availability may be varied each separately while leaving the others constant (see Fig. 2). After incubation, the cell densities on the sediment surfaces are evaluated by means of epifluorescence light microscopy or low-temperature scanning electron micros-copy (see below). Thus, data on the effects of these external parameters on the VM and species abundances become available.

FIGURE 1: Mini-mesocosms in aluminium stubs of 4 mm height and 10 mm diameter. The cavities are 3 mm in depth and 6 mm in diameter (A). Small aliquots of thoroughly homogenized sediment samples are transferred into the cavities of aluminium stubs (B). These can be placed in humid chambers under defined conditions of e.g. light, temperatur and salinity. After cryofixation, the stubs are mounted onto a specimen holder (C) and transferred into cryochamber attached to a scanning electron microscope.

LOW-TEMPERATURE SCANNING ELECTRON MICROSCOPY (LTSEM) AND EPIFLUORESCENCE LIGHT MICROSCOPY

LTSEM and epifluorescence light microscopy of aluminium stubs or small petri dishes filled with sediment allow the investigation of diatom migration and lead to similar results. LTSEM was first introduced for the investigation of Wadden Sea sediments by Paterson (1986) and allows the observation of sediments and diatoms living therein in an almost natural state. The fixation procedure of sediment samples during cryofixation was further improved by the development of the Cryolander device (Whiltshire et al. 1997). Using LTSEM, data on diversity and abundances of species covering the sediment surface be-come available (see Fig. 3A). If sampling is performed at regular intervals during a complete tidal cycle, it is even possible to deter-

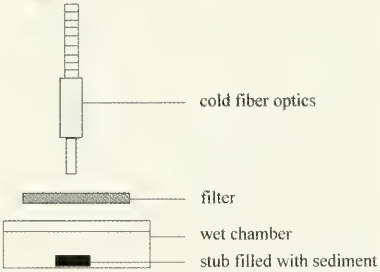

FIGURE 2: Experimental setup for investigating the effects of external factors on the VM. Small petri dishes or aluminium stubs filled with sediments are placed in a humid chamber. Light is supplied from above by using cold fiber optics. Gray or interference filters may be used to alter either light intensity or light quality. The temperature may varied by placing the wet chambers onto a cooling/heating device. Furthermore, the chambers can be flushed with gases via inlet/outlet ports (not shown in the figure).

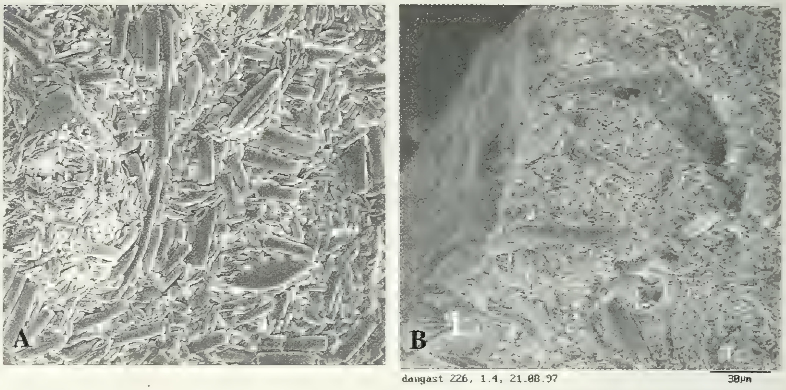

FIGURE 3: (A) Electron micrograph of a sediment surface visualized by LTSEM. Diatom cells dominate the surface. Beside, a filamenteous cyanobacterium can be seen. (B) LTSEM electron micrograph of a sediment sample which has been freeze-fractured perpendicularly to the sediment surface. The location and distribution of cells within the sediment bed become visible.

mine at which time distinct species show VM (Paterson 1986). The latter can also be done by epifluorescence light microscopy or by using the lens tissue technique of Eaton and Moss (1966). LTSEM, however, allows the collection of this information on natural sediments, which have been cryofixed in the field, or from those kept in mini-mesocosms (Janssen et al. 1999; Sauer et al. 2002). When sediment samples become freeze-fractured perpendicularly to the sediment surface, LTSEM even allows investigation of the location and distribution of cells within the sediment bed (see Fig. 3B).

Sauer et al. (2002) found that the migration of diatoms onto the sediment surface was partially inhibited by darkness but strongly enhanced by light. Inhibition and enhancement were reversible. These results are in accordance with data of Palmer and Round (1967) for *Hantzschia* sp. Increasing light intensities (up to 500 µmol photons m^{-2} s^{-1} were applied) led to rise in cell numbers on the sediment surface and resulted in variations in the composition of species migrating to the sediment surface; large species like *Gyrosigma* surfaced under low fluence rates whereas naviculoid species surfaced under higher fluence rates (Sauer et al. 2002). Changes in the composition of surfacing species have already been described by Round and Palmer (1966) and Paterson (1986). Sauer et al. (2002) found that the upward migration in the morning was most responsive to light. When the sediment samples were remixed or mixed around noon or in the afternoon, fewer cells migrated to the surface. Thus, it might be that the sensitivity to the light stimulus is highest in the early morning hours or immediately after tidal cover had drained off. A maximum upward migratory behaviour was found at 35 ppm salinity. Fewer cells surfaced when the salinity was either lowered or increased. Higher salinities might occur during hot and/or windy days and nights after prolonged exposure of the sediment surfaces whereas lower salinity values might be caused by rainfall or in inlets of estuarine waters.

Migratory speed is assumed to be an important factor responsible for the accumulation of the diatoms on the sediment surface. The migratory speed averaged over the entire diatom population was approximately 1 µm/s and remained similar during experiments in which salinity was either lowered to 5 ppm or increased to 60 ppm (Sauer et al. 2002). This value is rather low and does not necessarily reflect the migratory speed that diatoms will show when moving in natural substrates as the horizontal migration speed was measured in cuvettes. Hay et al. (1993) reported an average speed of 4.7 µm/sec for a *Gyrosigma* species over an artificial sediment surface (kaolin) but a much slower migration speed of 0.17 to 0.19 µm/sec. when the diatom moved through a sediment bed.

The light quality also has a great impact on the upward directed VM. Thus, diatoms surface most when illuminated with blue light; almost no response was registered under green light, whereas illumination with red light seems to have some positive effect on the migration onto the sediment surface (Wenderoth and Rhiel 2004). Several classes of photoreceptors with defined functions and absorbance characteristics have been described for plants, and the results indicate that most probably the cryptochromes, which absorb blue light, and the phytochromes, which absorb in the red light/far red light region, are involved.

TIME-LAPSE VIDEO MICROSCOPY

Time-lapse video microscopy is another excellent tool to study the migration behaviour, i.e., migratory speed and migration on/in natural/artificial sediments or horizontal cuvettes. Individual cells or cell assemblages can be tracked for hours and days. Although LTSEM finally results in cryofixation and death of living cells, time-lapse video microscopy allows investigations without damaging them. Single pictures and videos can be recorded using framegrabber software and hardware and stored as digitized files (pictures as TIF or JPG formatted files, video clips as MPG or AVI files) on a personal computer (Sauer et al. 2002). An example is given in Figure 4. It shows that the trails of individual large cells, most probably species of the genera *Pleurosigma* or *Gyrosigma*, were used by other, smaller diatoms, most probably *Navicula* species, for upward directed VM (Wenderoth et al. 2004). The movement of three large diatoms was monitored. One cell moved up and down the cuvette on the same trail, from the upper to the lower edge of the screen before it disappeared at the lower left corner. Its trail was used by smaller cells for upward migration. The other larger cell moved from the upper to the right edge where it disappeared. Later, a third large cell, which may or may not be the same individual as the second one, moved in from the right edge and formed a new trail moving downwards and upwards before it disappeared in the lower right corner. It was followed by smaller cells, which soon afterwards used all the trails formed by the large cells for upward VM.

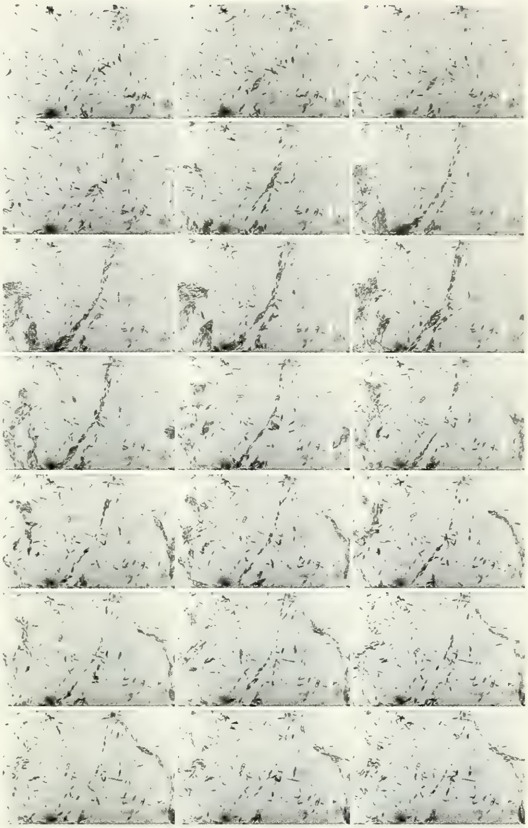

FIGURE 4: Images taken by time-lapse video microscopy showing the movement of diatoms in the vertical cuvette. For the video documentation, a small amount of sediment was placed onto the bottom of a home made cuvette which was positioned vertically in front of a horizontally fixed light microscope. The cuvette was floated with artificial seawater and illuminated from above. Near infrared light for video microscopy was provided by a projector using a 740 nm interference filter. The migratory behaviour of diatoms was documented immediately above the sediment sample in the cuvette over a time period of 24 hours using a 12.5× Leitz achromatic objective in combination with a Panasonic B/W CCD camera and a time lapse video cassette recorder. The video tape was digitized on a personal computer to an AVI file. Representative single pictures taken from the video clip are shown with the first one in the upper left and the last one in the lower right corner of the figure. The area size of the pictures is 700 μm × 500 μm.

NUCLEIC ACID AND PROTEIN WORK

Endogeneous rhythms in gene expression as well as short-term adaptation processes on external factors such as fluctuating light intensities will result in fluctuating mRNA and polypeptide abundancies. The polypeptides, constituting the light-harvesting (LH) complexes, are an excellent starting material for studying gene expression and protein quantities of Wadden Sea-inhabiting diatoms. Both the genes encoding LH polypeptides (*lhc* genes) and the LH polypeptides and their mRNAs are highly abundant and have already been investigated in detail in higher plants and green algae: lhc genes exhibit an endogenous circadian rhythmic expression pattern with increasing amounts of mRNA from the onset of light towards noon and decreasing amounts in the afternoon towards night. This expression pattern results in almost concomitant enhanced amounts of newly synthesized LH polypeptides in the morning and reduced synthesis in the afternoon. *lhc* mRNA and LH polypeptide abundancies are further regulated by external factors such as light (intensity and quality), temperature, and nutrient availability. In diatoms, the counterparts to the *lhc* genes and LH polypeptides of higher plants and green algae are the *fcp* genes and their corresponding gene products, the fucoxanthin chlorophyll *a/c* binding polypeptides (*Fcp*). Data on *fcp* gene expression and *Fcp* abundancies are rare and almost restricted to laboratory studies. Eight *fcp* genes of the centric diatom, *Cyclotella cryptica*, have been cloned from a cDNA library and investigated in detail (Eppard and Rhiel 1998; Eppard and Rhiel 2000; Eppard et al. 2000). Phylogenetic analyses show that they can be grouped into three distinct clusters. Cluster I harbours the *fcp* genes *fcp1, fcp2, fcp3* and *fcp5*. They are similar to the *fcp* genes known from other diatoms and brown algae. Cluster II contains the *fcp* genes *fcp6, fcp7* and *fcp12*, which are more closely related to light-inducible *lhc*-related genes, which have been cloned from the green alga, *Chlamydomonas*. In cluster III, currently one *fcp* gene, *fcp4*, has been placed which shows the highest homology to the *lhc* genes cloned from the red alga, *Porphyridium cruentum*. The transcript sizes of fcp genes of *Cyclotella cryptica*, belonging to different *fcp* gene clusters and encoding different *Fcps*, the diurnal expression of the *fcp1/fcp2/fcp3/fcp5* gene cluster and the steady-state mRNA concentrations of all gene clusters in response to light quality and quantity were investigated by Oeltjen et al. (2002). The mRNAs of the gene cluster I are approximately 950 bases in length, whereas those of the *fcp4* and the fcp6/fcp7/fcp12 clusters are approximately 1050 (*fcp4*), 880 (*fcp6/fcp7*) and 1150 (*fcp12*) bases in lengths. Similar to what is found for higher plants, the steady-state mRNA concentration of the *fcp1/fcp2/fcp3/fcp5* gene cluster increased with the onset of light, reached a maximum around noon and dropped in the afternoon. The steady-state mRNA concentrations of the genes belonging to cluster I and of the *fcp4* gene were higher when *C. cryptica* was grown in low light, whereas the steady-state mRNA concentration of the *fcp6/fcp7/fcp12* gene cluster increased under high light growth conditions. The steady-state mRNA concentrations of all gene clusters were highest when *C. cryptica* was grown in red light, intermediate in green light, and lowest in blue light. The *fcp* genes, especially those belonging to the gene cluster I, and a polyclonal antiserum raised against the *Fcps* of *C. cryptica* are excellent tools for studying steady-state fcp mRNA concentrations and *Fcp* abundances of diatoms directly in the field. The methodological approaches were published by Hust et al. (1999) and Meyer et al. (2003); they are summarized in the flow chart of Figure 5.

Generally, the results using these techniques are in line with those obtained in laboratory experiments on unialgal cultures. Hust et al. (1999) found that repetitive extractions with sodium dodecylsulfate (SDS) containing sample loading buffer used for SDS-polyacrylamide gel electrophoresis ensured that more than 98% of the extractable protein was recovered. Subsequent Western immunoblotting with the *Fcp*-antiserum selectively immunodecorated *Fcps* and, thus, demonstrates that a taxon-specific class of polypeptides can be visualized and quantified directly

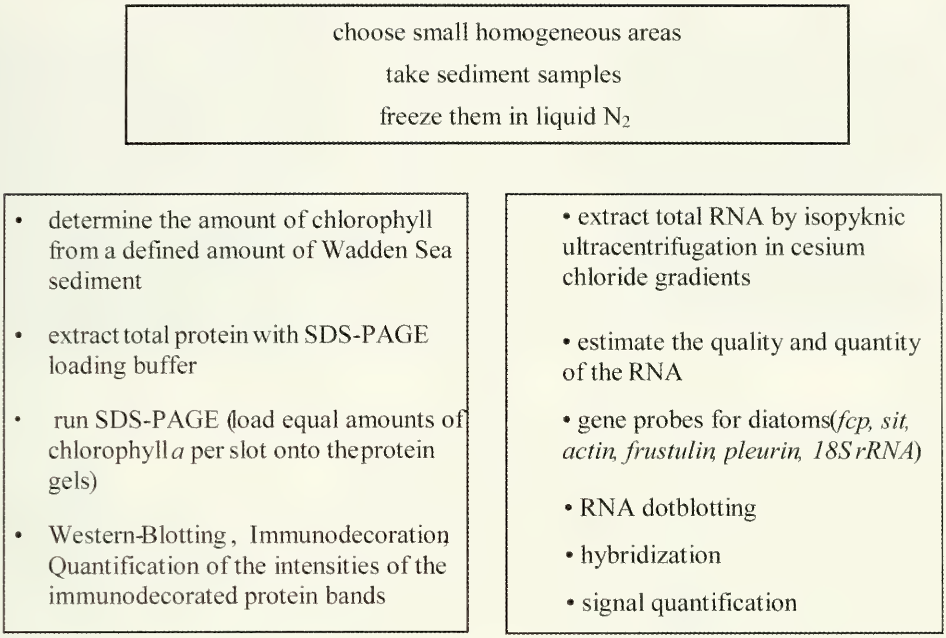

FIGURE 5: Flow chart for the isolation of total protein (left) or total RNA (right) out of Wadden Sea sediments.

in sediment samples. In shading experiments, shaded sediment areas generally revealed higher amounts of *Fcp* subunits which could be immunodecorated.

Meyer et al. (2003) established a method to investigate the steady-state levels of *fcp* mRNAs of diatoms *in situ*. Field samples were taken after tidal exposure from dawn to late afternoon at two-hour intervals and frozen in liquid nitrogen. In the laboratory, total RNA was isolated by isopyknic ultracentrifugation in cesium chloride gradients. Defined amounts of total RNA were blotted onto nylon membranes and hybridized with probes against the *fcp2* and 18S rDNA genes of *C. cryptica*. The steady-state amount of *fcp* mRNAs was estimated by normalizing the *fcp* signal intensities to the signal intensities obtained from hybridization experiments, in which the 18S rDNA gene probe was used (see flow chart, Fig. 5). In time course studies, which were performed to demonstrate the applicability of the method, the steady-state levels of *fcp* mRNA increased up to 12-fold with the onset of light. Similar to what has been found in laboratory experiments on unialgal cultures, the levels reached a maximum 6–8 h after sunrise before they decreased again. Further results using the methodological approaches described above are given in Figure 6. Here, Wadden Sea sediments were withdrawn during the morning hours up to 2 pm in the afternoon and subjected to RNA and protein isolation. For both the *Fcp* abundances and steady-state *fcp* mRNA concentrations, an increase towards the early afternoon could be demonstrated.

FUTURE PROSPECTS

At present, neither the effects of chemical gradients (O_2, CO_2, S^{2-}, NO_3^-) nor the impact of physical gradients such as temperature and pH on the VM have been investigated. The influences of excessive light (> 500 μmol photons m^{-2} s^{-1}) and gravitaxis on the VM have not been elucidated either. Further experiments have to be undertaken to unravel the individual impacts of the entire set of these factors.

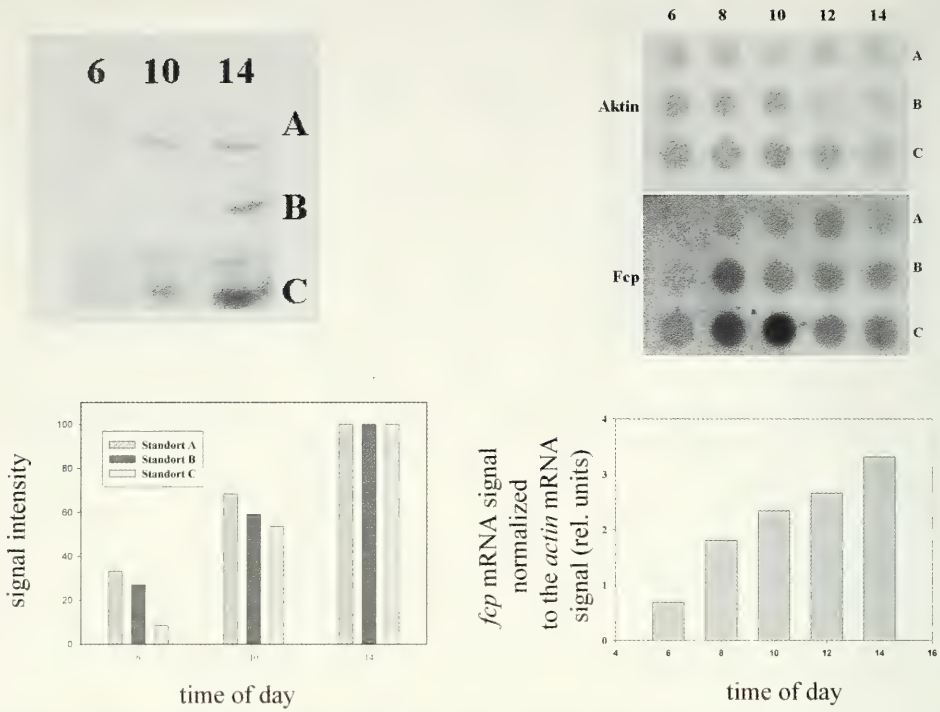

FIGURE 6: Left side, upper part: Western immunoblots of total protein extracted from three sediment sampling sites (A, B, and C). Sampling was performed at 6 am, 10 am and 2 pm, respectively. The proteins were blotted onto nitrocellulose after electrophoresis and immunolabeled with an antiserum directed against the Fcp subunits of the diatom *C. cryptica.*

Left side, lower part: The signal intensities obtained from quantitative analysis of the immunodecorized bands are presented as bars and plotted against the time of day; the highest signal intensity is set to 100 %.

Right side, upper part: Representative dot blots of 10 µg RNA isolated from three Wadden Sea sediment sampling sites (A, B, and C) and hybridized with either the fcp2 gene probe or the actin gene probe. The values above the dots show the local time of sample withdrawal. The gene probes are indicated on the left.

Right side, lower part: Bar graph showing the steady state level of Wadden Sea sediment fcp mRNA, which was estimated by normalizing the fcp signal intensities to the corresponding actin mRNA signal intensities. Abscissa: time of day, ordinate: normalized steady state fcp mRNA levels.

Additional molecular techniques have to be adjusted and applied: total DNA and RNA can be isolated from sediment samples which is suited for polymerase chain reaction (PCR-) mediated amplification of diatom-specific 18S rDNA or mRNA after being reverse-transcribed. The PCR products could be used for standard molecular techniques such as Single Stranded DNA Conformation Polymorphism (SSCP), Denaturing Gradient Gel Electrophoresis (DGGE), or Differential Display. The PCR products can be subjected to routine DNA sequencing protocols to yield information on the species from which they were derived as well as on species diversity. *In-vivo* cell labelling, in combination with confocal light microscopy, will allow tracing of individual species within their natural habitat by using species-specific gene probes derived from the sequencing data and carrying a fluorescence label. Antisera directed against proteins that play major roles in main enzymatic pathways (e.g., uptake of nitrate, phosphate, silicate, synthesis and excretion of polymers) will allow a closer look at protein abundancies, whereas the corresponding gene probes will allow conclusions on gene expression.

Diatoms are fascinating microorganisms. It is no matter of debate that they have attracted the attention of "observing and describing" scientists first: microscopists and taxonomists. As new methods, i.e., molecular, biochemical, and biophysical, have become available, it is — also no matter of debate — a challenge and chance to use these on diatoms in their natural habitats as well. In the future, modern methods will allow testing of species concepts and will surely yield information on how diatoms live and survive in their natural habitats.

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The Sino-Siberian Distribution of *Eunotia clevei* and its Relatives, from Lake Baikal to the Mekong Delta: The Union of Taxonomy, Biogeography, and Ecology

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In discussions of the interface between taxonomy and ecology one area emerges of prime importance: Biogeography. Whereas taxonomy deals with the grouping and naming of organisms and ecology deals with the parameters required for an organism to exist, biogeography explores the reasons why different biota come into being. In this paper we first review the status of taxonomic descriptions, in an attempt to quantify the information already available for use in biogeographic analyses. Second, we briefly describe two distinct patterns of distribution relative to the Lake Baikal diatom flora based on species in the *Eunotia clevei* species group.

In a recent issue of *Diatom Research*, Kociolek and Stoermer (2001) presented some thoughts concerning the integration of diatom taxonomy and ecology, two subjects that have different and possibly diverging objectives. Kociolek and Stoermer spoke of a 'marriage of necessity', a desire to unite the two subjects with a common purpose or, at the very least, to identify areas that might be thought of as contributing to a common aim. One might meaningfully ask a more general question, addressing the purpose of both disciplines but that would lead into largely philosophical discussions, having limited practical value in driving forward these two branches of science in diatom biology. The purpose of this collection of papers is to identify areas that might be understood as ways forward, rather than outlining differences of opinion over the relevance or otherwise of ecology and taxonomy to each other.

Our remarks below will address the issues as we see it and, although no doubt less than comprehensive, we happen to believe that there is one very practical way to pursue common goals, of benefit to a wide variety of disciplines including evolutionary studies as well as taxonomy and ecology.

Kociolek and Stoermer included five possibilities under their suggestions for areas in which 'correct' taxonomy might impact ecology:

Alien species
Comparative autecology
Comparison across space
Comparison across time
Biogeography

Here we are concerned with the last three, which are interrelated. The third topic above, 'Comparison across space' and the fourth, 'Comparison across time,' may dovetail nicely into the fifth, 'Biogeography,' which in our view is where the future union of taxonomy and ecology lies (Kociolek and Spaulding 2000).

‘COMPARISONS ACROSS SPACE’

Kociolek and Stoermer subdivided ‘Comparisons across space’ into three parts:

- Floras
- Monographs
- Specimens

In diatom taxonomy (and probably throughout comparative botany), there are fewer monographs than floras, simply because, whereas the scope is narrow, detail is not. Both enterprises, monographs and floras, produce a wealth of data, primarily in the form of illustrations of specimens, secondarily in the form of associated data. Below we present a few figures that might help with some focus.

Floras

First, how might one understand the content of floras? A general view is difficult, in that they can vary in content and execution. Some might take many years to complete and, when published, are composed of many volumes. The *Seaweeds of the British Isles*, for example, will probably be complete in 2005, the first volume being published in 1977, with six further volumes each devoted to a particular algal ‘group’ (sadly, lacking a diatom volume) (Dixon and Irvine 1977, 1995); Irvine 1983; Christensen 1987 (1995); Fletcher 1987; Burrows, 1991; Maggs and Hommersand 1993; Irvine and Chamberlain 1994; Brodie and Irvine 2003). Such comprehensive works are usually undertaken by a number of people, some of whom may end up devoting most of their working lives to completing their particular taxonomic treatment.

The most comprehensive European diatom flora appears in the *Süsswasserflora von Mitteleuropa* series, primarily undertaken by two diatomists, Horst Lange-Bertalot and Kurt Krammer. It is principally composed of four volumes spanning a 5-year publishing period (1986–1991), with a 5th volume providing taxonomic keys in French and English and a 6th volume, a revised edition of 2(3), both published in 2000 (Krammer and Lange-Bertalot 1986, 1988, 1991a and b, 2000a and b). The first four volumes include roughly 650 plates, each plate having, on average, 20 illustrations, giving a rough total of 13000 images in all.

In contrast, most diatom floras are usually less broadly conceived, containing detailed accounts of taxa found in a particular area, accompanied by notes (where necessary), descriptions of new taxa (if any), an illustration or two and maybe some reference to the herbarium (or other collection) where the specimens can be found. On average, floras of this kind have between 30 and 50 plates, each plate having 10–20 separate pictures, giving a total of between 300 and 1000 illustrations per flora.

If five floras of this kind were published per year, then over a 5-year period, the 25 floras would contribute some 25000 illustrations — an impressive amount of data.

Monographs

Half a century ago Robert Ross wrote a little on the subject of diatom monographs. He noted that “Very little monographic work has been done on the Diatoms during this century and only a few small genera have been dealt with. Almost the whole group is in need of taxonomic revision…” (Ross 1951:142). Up until the mid-1980s there were few works that could be called monographic. Since that time things have changed. For example, of the 46 volumes in the *Bibliotheca Diatomologica* series, eight are monographs, devoted to a particular genus or a section within a large genus. The series has a publishing history from 1983 to the present, roughly 20 years. By definition monographs will vary and it might be futile to generalise about the number of illustrations. Nevertheless, as an example, consider Krammer's monograph on Cymbelloid genera (Krammer 1997a, b). Published in two volumes, this work presents a total of roughly 950 printed pages, of which more than 300 are illustrations. At an average of 15 pictures per page, there is something in the region of 4500 pictures.

Specimens

The calculations given above for published illustrations are very approximate but give some indication of the volume of data available for taxonomists, even with the meagre amount of time diatomists have to devote to this kind of work.

The one factor common to both enterprises, floras and monographs alike, is that no matter how well (or poorly) documented the taxa are in the final publication, all these data must have been based on specimens of one kind or another. So where are those specimens now? Again, it might be easy to peruse the publications and trace the herbarium or collection to which the samples were eventually deposited (in a certain number of cases that might not be possible).

The storage and retrieval of these data to one side, what is again inescapable is their abundance. But what of its relevance, which might seem opaque, other than simply documenting either one group of diatoms or one particular area or region? Usually, at least for diatomists, these works (floras in particular) are seen as aids to further scientific study, as guides to the organisms that inhabit an area — perhaps a starting point for generalisations to be made concerning issues of their ecology. How might these data be brought to bear on any particular problem, any particular biological problem?

One purpose of this meeting was to detect or suggest ways in which two potentially 'symbiotic' disciplines of taxonomy and ecology might contribute to something bigger than each on its own. That might be biogeography, the study of the distribution of organisms and their relation to Earth history. And biogeography is where the data of monographs and floras intermingle and gain meaning – irrespective of how poor the ecological data might be, every organism occurs somewhere and that information is almost always recorded.

LAKE BAIKAL: AN EXAMPLE OF FLORISTIC NECESSITY VERSUS MONOGRAPHIC REQUIREMENT

Lake Baikal in western Siberia is a well-defined area and, conceivably, might yield more of general relevance via floristic studies than other less well-defined areas, such as New Zealand, or more precise than Northumberland, in the UK, as two extreme examples — both of which have published floras (Donkin 1858, 1861, 1869; Cassie 1989). The latter two areas may simply indicate political boundaries rather than biological regions. That suggests another significant problem. What are biological regions? This question is relevant to comparative biology as a whole and one we do not address further here (but see Williams and Ebach 2004).

Lake Baikal does not really have a comprehensive flora, in spite of many papers published over a period of nearly 100 years. Nevertheless, the available data do provide a kind of snapshot. From the floristic point of view, a snapshot is about the best we can do.

Consider the contributions of Boris Skvortzov. He published two large papers on the diatoms of Lake Baikal. The first paper, published in 1928, was a preliminary survey (Skvortzov and Meyer 1928). That survey was based upon just 36 samples (Williams 2004). His second paper, published

10 years later, was a more detailed examination of just one of those 36 samples (Skvortzov 1937a). From Skvortzov's study, one might hazard an estimate of Lake Baikal's benthic diatom diversity. By his estimate there are roughly 450 taxa present (452 in Skvortzov 1937a). Of those, Skvortzov's figures suggest, by inference, that 304 are cosmopolitan and 148 endemic (the endemics were described by Skvortzov). By cosmopolitan, we mean simply that some taxa were described prior to Skvortzov's work and hence are known from some other locality. If these figures mean anything, they suggest that roughly one third of the flora is endemic to Lake Baikal (Williams and Reid 2003). But Skvortzov did not see the 304 non-endemic taxa as truly cosmopolitan, in the sense they occured everywhere else on the globe. He adopted a particular way of understanding the flora by dividing the species he recognised into five groups:

(A) Siberian and sub-alpine elements
(B) Tertiary freshwater remains and tropical origin
(C) Marine elements or marine relicts
(D) Brackish-water species
(E) Elements of indistinct origin

At first sight Skvortzov's groupings are a little puzzling, as they appear to be a mix of geography, history and ecology. For instance, it is quite possible for a taxon to be a marine relict (C) as well as of tropical origin (B). One might adjust Skvortzov's groups to align them with just one parameter, even if that parameter is broadly construed. One might assume that category (A), although defined geographically, may be equated with species present only (and always) in 'cold' freshwater habitats. Category (B) might be construed to refer to species once believed to have been tropical (warm water species) but are not so now. Categories (C) and (D) might be construed to refer to a previous existence, where the species in question once dwelt in either a marine (C) or brackish (D) environment and now do not. Category (E) may be safely ignored as of no real meaning. Surprisingly, Skvortzov wrote of this last category that it "is represented by a large series of Baikal endemics to which I have not yet found relationships" (Skvortov 1937a:298). In other words, many of the Lake Baikal endemics could not be easily related to the five groups. Skvortzov simply did not know what to do with them.

This might be a fair summary of Skvortzov's divisions. But it is also instructive to know that he based them upon a previous scheme, drawn up by Vereshagin in the early 1900s based, in part, on work undertaken by Lev Berg, a talented, but now almost forgotten, Russian ichthyologist and evolutionary biologist (see Skvortzov 1937a:295; Berg 1926). How useful are Skvortzov's divisions today? Probably not much — one has to work quite hard to derive any real meaning from them. Perhaps also, his ideas belong to a bygone era, one in which ecology was not particularly uppermost in peoples' minds, or at least not particularly well-defined (Flower, this volume).

These comments are not intended as critical of Skvortzov, Vereshagin or Berg. We simply wish to draw attention to one aspect of possible misunderstanding between diatom ecologists and taxonomists, one that remains today. Skvortzov had a purpose. His reasons for the sub-divisions were an attempt to explain the *origin* of Lake Baikal's diatom flora; *origin* in terms of where the present day taxa may have come from. It is worth quoting Skvortzov at length, as his own words explain his purpose:

"The present study shows a certain similarity of the Baikal diatoms to those of Tanganyika Lake, Africa; to Neogene freshwater floras of Nippon [Japan]; to Tertiary diatom floras of Hungary; to the recent flora of Demerara River, Paraguay [*sic*], South America; and to some forms widely represented in oceans. All this can be explained only by the help of Prof. G.I. Wereschtschagin's theory of the origin of the Baikal fauna and flora" (Skvortzov 1937a:298).

We may abstract from this statement (along with the five categories above) two kinds of information: geography and, broadly speaking, ecology. Skvortzov's ecology might be thought of as simple; he is really talking about four broad 'categories': (A) cold-water, (B) tropical water, (C) marine, and (D) brackish. His geography is somewhat more puzzling, as it includes Europe, Africa, Japan, South America and the world's Oceans. Taken together, they lack precision: Lake Baikal diatoms are related to organisms somewhere in the rest of the world, be that Hungarian fossil deposits or Lake Tanganyika in Africa. But the general message is interesting and has been little exploited in recent years. What other areas of the world are the diatoms of Lake Baikal related to? And what can be said of the environments that make up those areas? Buried in Skvortzov's prose is the essence of comparative biology. What relationships can be specified, first by the organisms themselves, second by where those organisms live. So where did Lake Baikal's diatom flora come from? Here we see the problem illuminated via individual taxa, or more precisely, via individual groups of taxa.

Previously, we examined species in the genus *Tetracyclus* (Williams et al. 2002) and its patterns of distribution in Lake Baikal (Williams 2004). Here we deal briefly with species from the genus *Eunotia* Ehrenb. We chose this genus for a number reasons. First, it is large and diverse with perhaps over 1200 species, distributed globally. Second, within that 1200 species, a fair number are endemic to different parts of the world. Third, the genus is well defined, with the arrangement of raphe and rimoportulae quite unique among diatoms (Kociolek 2000). Fourth, it has a well-defined ecological niche, rarely if ever, does it occur in habitats that are not acidic.

THE GENUS *EUNOTIA* IN THE SINO-SIBERIAN REGION

Skvortzov believed that there were 30 cosmopolitan taxa belonging to *Eunotia* in Lake Baikal, of which 12 have a fossil record. There are 11 endemic taxa belonging to *Eunotia*, of which four have a fossil record, roughly one third being endemic, similar to the entire flora, with half of those having a fossil record. Skvortzov listed just two taxa from *Eunotia* (*E. praerupta* and *E. praerupta* var. *inflata*) as a 'Siberian and Subalpine element,' and three species (*E. mondon*, *E. clevei* and *E. lacusbaikalii*) of 'Tertiary freshwater remains and tropical origin' but placed no species in the group of 'Marine Elements or Marine Relicts.' In a general sense, the last two categories are of interest: the possibilities of tropical relatives and the possibilities of marine environments.

Among the species of *Eunotia*, *E. clevei* and its morphologically similar relatives have recently been revised (Williams and Reid 2005). This species complex is of some significance, from the perspective of ecology as well as taxonomy. First, it is structurally different from other species of *Eunotia* (Vyverman et al. 1998; Edlund et al. 2000; Reid and Williams 2001) and second, it is never found in acidic waters. In fact, both ecologically and morphologically it is quite atypical. We have described a new genus to accommodate this species complex. The revised taxonomic views do not affect the general argument presented here (Williams and Reid 2005).

Skvortzov placed *Eunotia clevei* in the 'Tertiary freshwater remains and tropical origin' category. It is useful to sub-divide Skvortzov's category (B) 'Tertiary freshwater remains and tropical origin' into "tertiary relicts" and "tropical origins." Skvortzov suggested the 'Tertiary freshwater remains and tropical origin' group for *E. clevei*, as it is found in Sweden, Finland, Russia, and Mongolia, and known as a fossil from the USA, Japan, and China. With knowledge of these distributions there is the suggestion that *E. clevei* is indeed a relict, Tertiary or otherwise, *but* its presence in China suggests a tropical component as well as a marine environment (see below).

"TERTIARY RELICTS."— In Lake Baikal there are several 'kinds' of *Eunotia clevei*. There is the typical species, known from elsewhere in the Northern hemisphere (Reid and Williams 2001;

Edlund et al. 2000). In addition, Skvortzov identified and described two new varieties, *baicalensis* and *hispida* and one new species, *Eunotia lacusbaikalii*, similar in morphology to *E. clevei*. *E. clevei* var. *baicalensis* and *E. lacusbaikali* seem to be both truly endemic to Lake Baikal and therefore 'Siberian and Sub-alpine'. *Eunotia hispida* has been considered a Lake Baikal endemic but appears to be present in Lake Onega and, as a fossil, Lake Ladoga in Finland, and seems also to be a 'Tertiary relict' (Reid and Williams 2001).

Elsewhere in Russia, Moisseeva described another variety, *E. clevei* var. *aculeata* Moisseeva (Moisseeva 1971) and, in another publication, Lupikina and Dolmatova (1982) described two species, *Eunotia maculata* Lupikina and Dolmatova and *Actinella penzhica* Lupikina and Dolmatova, both having morphological similarities to *E. clevei*, suggesting a close relationship. Therefore, in the Boreal (cold-water) parts of the Northern Hemisphere there are several entities that appear to belong to one complex, related directly to *E. clevei* (Table 1). What is of significance is that if the ecology is separated from the geography, then some greater precision is possible in specifying the taxa and the places they live.

TABLE 1. Species of '*Eunotia*' *clevei* associated with Skvortzov's 'Tertiary freshwater remains…', the first pattern. All species belong to a new genus, to be described (Williams and Reid 2005).

Northern Hemisphere: 'Tertiary freshwater remains	
Eunotia clevei Grunow	"Northern Hemisphere"
Eunotia hispida (Skvortzov) Reid & Williams	Lake Baikal (and elsewhere)
Eunotia clevei var. *baicalensis* Skvortzov	Lake Baikal
Eunotia lacusbaikali Skvortzov	Lake Baikal
Eunotia clevei var. *aculeata* Skvortzov	"Primorskii Krai"
Eunotia maculata Moiseeva	Kamchatka
Actinella penzhica Lupikina & Dolmatova	Kamchatka

TABLE 2. Species of '*Eunotia*' *clevei* associated with Skvortzov's 'tropical origin…', the second pattern. All species belong to a new genus, to be described (Williams and Reid 2005).

Northern Hemisphere?? ('…tropical origin')	
E. americana var. *asiatica* Voigt	Canto and Shanghai
E. reimerii Williams & Reid	West River
Eunotia botuliformis Wang (non *E. botuliformis* Nörpel-Schempp & Lange-Bertalot)	Pearl River, South China
Eunotia pseudoclevei Wang	Pearl River, South China
E. clevei var. *obliquestriata* Qi, Lin et Hi	Hubei Province
E. clevei var. *sinica* Skvortzov	Foochow, South China
Actinella miocenica Li	Jiling Province

"TROPICAL ORIGINS."— What of other specimens possibly related to *E. clevei* but described from elsewhere? Skvortzov named and described another variety of *E. clevei*, *E. clevei* var. *sinica*, from China (Skvortzov 1929). A little later he changed his mind and declared his new variety a synonym of *E. clevei*, a hasty judgement in our view (Skvortzov 1937b; Reid and Williams 2001; Williams and Reid 2005). Since that time six further species have been named, all with morphological features that suggests a close relationship to *E. clevei*; and all occur in marine or brackish waters (Voigt 1969; Qi et al. 1986; Shi 1991, 1997; Wang 1998) (Table 2).

So what we have is a diverse assemblage of *Eunotia clevei*-like specimens in Lake Baikal — Northern Hemisphere relicts — and a second group of *Eunotia clevei*-like specimens in and around the tropical parts of China and possibly South-east Asia. The details of all the species from these areas are not yet well known but separating their geography from their ecology helps a little with identifying the complex factors required to explain their origin relative to the entire Lake Baikal diatom flora, and possible its entire fauna and flora.

SUMMARY

First, none of the *E. clevei* group of species occurs in acid waters, so they are very different from the usual species in *Eunotia*. Second, the 'tropical' specimens are, more or less, marine or brackish. Third, two patterns of distribution seem to be emerging: One in the Northern hemisphere, the other extending towards the tropics. Although data on their distribution are sparse, the pattern of extinction and survival is not too opaque to be lost forever.

If the unique elements of taxonomy, ecology and geography are separated out and dealt with in their own terms, then their marriage, or reunion, is likely to be more harmonious. Given the abundance of taxonomic data already available it is possible to select genera for investigation in the geographical dimension — and thereby identifying problematic taxa. Only by knowing exactly what each discipline can contribute to a particular problem — in this case biogeography and the origins of the Lake Baikal diatom flora — can progress be made on the understanding of how and why diatoms species became so diverse, occupy so many different niches and continue to flourish.

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